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UNIVERSITY OF ALBERTA

AUTUMN AND WINTER MOVEMENTS AND MORTALITY OF WILLOW PTARMIGAN AT CHILKAT PASS, B.C.

by

ROGIER C. GRUYS ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING 1991

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the faculty of Graduate Studies and Research for acceptance, a thesis entitled AUTUMN AND WINTER MOVEMENTS AND MORTALITY OF WILLOW PTARMIGAN AT CHILKAT PASS, B.C. submitted by ROGIER C. GRUYS in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

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Aan mijn ouders

ABSTRACT

I studied the timing and extent of movements and mortality of adult willow ptarmigan at Chilkat Pass, B.C. during autumn and winter. Radio-tagged ptarmigan did not leave their breeding grounds immediately after broods broke up, but remained on or near their territories until December. After chicks fledged, part of the population moved uphill from their territories. In late September, coincident with molt into winter plumage, ptarmigan moved farther from their territories. Both movements were presumably to areas with better cover and/or food. Once they molted, all tagged adult males and half of the tagged females returned to their territories, and males resumed territorial display. Ptarmigan remained on their territories until increasing snow cover depleted food and cover, forcing them to leave. Males left the breeding grounds later than females, and returned earlier in spring. In winter females moved farther than males, but several males moved as far as females.

Natural autumn and overwinter mortality of adult males and females was similar in both years of the study. Adult females suffered most mortality during autumn raptor migration and on their wintering grounds. Adult males were killed during autumn and spring raptor migrations, as well as on the wintering grounds. Birds wintering in subalpine and forested habitats suffered similar mortality. During the breeding season female mortality ranged between 5 and 26%, mostly during incubation and after chicks hatched. In contrast, males suffered negligible mortality after they settled on their territories. Hence, differential mortality between the sexes occurred during the breeding season.

Hunting mortality of banded birds was less than 20% in each of ten years. Banded males and females suffered similar hunting mortality each year. Among unbanded birds, males predominated in the hunters' bags even when females were still

in the areas frequented by hunters. Hence, sex and age ratios from hunters' bags are an inaccurate estimator of true population composition.

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CHAPTER 1 THESIS INTRODUCTION

The factors determining successful reproduction differ between males and females; ultimately breeding success of males depends on access to mates, whereas success of females depends on acquisition of resources for reproduction. As a result, selectional pressures on males and females differ widely in many species (Bateman 1948; Clutton-Brock et al. 1982). Some authors have even treated the sexes as if they were different species (Trivers 1972). In many species of birds and mammals, males and females are segregated during most of the year, except for a brief period during the mating season. In some species males remain with their mates throughout the rearing of offspring, but segregate once offspring are independent (e.g. willow ptarmigan (Lagopus lagopus; Wittenberger 1978), whereas in extreme cases males and females associate with one another only to mate (e.g. lekking grouse; Wittenberger 1978).

Male and female willow ptarmigan are thought to be segregated throughout the winter; most males appear to remain in subalpine habitat, whereas most females apparently move to the boreal forest (Weeden 1964; Irving et al. 1967; Höhn 1984). As a result, each sex can be exposed to different environmental conditions (Clutton-Brock et al. 1982). For willow ptarmigan, weather may differ between wintering habitats of males and females, which could cause higher mortality in one of the sexes (see e.g. McGowan 1975). Ptarmigan that move to the boreal forest may compete for food with snowshoe hares (Lepus americanus). Both willow ptarmigan and snowshoe hares in North America undergo cyclic fluctuations in numbers with a periodicity of 8-11 years (Bergerud 1970; Hannon and Barry 1986; Krebs et al. 1986; Mossop 1987). It has been suggested that predators in the boreal forest switch to grouse when populations of hares or voles decline (Rusch and Keith 1971; Hörnfeldt

1978; Angelstam et al. 1984). Hence, females wintering in the boreal forest may suffer higher mortality. On the other hand, male ptarmigan often suffer higher hunting pressure (Bergerud 1970; Braun and Rogers 1971; Weeden 1972; Bergerud 1987). Although this predominance of males in hunters' bags could be caused by differential natural mortality of the sexes before the hunting season, it is more likely due to segregation of the sexes (Braun and Rogers 1971, see Zwickel 1982). Such differences in environmental conditions or mortality could result in a shortage of members of one sex, as has been observed in populations of willow ptarmigan (Martin 1985; Hannon and Barry 1986), as well as other species of grouse (e.g. Zwickel et al. 1983; Angelstam 1984). However, Mossop (1987) observed that willow ptarmigan at Chilkat Pass, B.C. did not move from the breeding area until February, and in a year with little snow most females remained near the breeding grounds. These observations suggest that the period of segregation may vary annually. As a result, the difference in environmental conditions to which males and females are subjected each year is likely to vary, and with it differences in survival rates.

Most losses of ptarmigan occur outside the breeding season (Bergerud 1987). It has been argued that overwinter mortality plays a role in regulating grouse numbers (Gullion 1970). Hunting mortality may be partly additive to natural mortality (Myrberget 1985). Thus, to understand the role mortality plays in population regulation, it is essential to examine both natural and hunting mortality during the non-breeding season, and determine what causes them to vary between years and sexes.

1.1 This study

Observations of differential natural and hunting mortality on willow ptarmigan have been published (Hannon and Barry 1986; Bergerud 1987), and there are reports on the timing and extent of ptarmigan movements during winter (Weeden 1964; Hoffman and Braun 1975; Höhn 1984; Gardarsson 1987; Mossop 1987). However, there has been no effort to integrate the causes of differences in overwinter losses with variations in winter movements between the sexes. This is partly due to the fact that to date most studies documenting winter movements and mortality of ptarmigan used counts and/or band recovery data. Although these methods can provide estimates of distances moved and total mortality levels, they cannot explain the underlying causes. With the advent of radio telemetry, however, it has become possible to follow individual ptarmigan from one breeding season to the next and document their fates.

In this thesis I report on a study at Chilkat Pass, B.C. in which I equipped adult willow ptarmigan of both sexes with radio transmitters during the summers of 1987 and 1988. I followed these birds throughout the following winters to determine if differences in movements and habitat selection between the sexes resulted in differential mortality. To examine the causes of ptarmigan winter movements I related their movements to snow depth, vegetation height, and weather data. I present the results in three chapters. In the first chapter I document the movements and habitat use of radio-tagged male and female adult ptarmigan outside the breeding season. In the second chapter I discuss the rates of natural mortality radio-tagged ptarmigan suffer during the non-reproductive season, and compare them to predation rates during the breeding season. In the third chapter I determine the sex and age ratios of ptarmigan in hunters' bags, and document hunting mortality of banded ptarmigan.

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CHAPTER 2 AUTUMN AND WINTER MOVEMENTS OF WILLOW PTARMIGAN AT CHILKAT PASS, B.C.

2.1 INTRODUCTION

Segregation of the sexes in the non-breeding season is common among both mammals (Clutton-Brock *et al*. 1982) and birds (Myers 1981). Three hypotheses have been framed to explain the causes underlying this segregation among birds: 1. intersexual competition for limited resources causes the subordinate sex to travel farther from the breeding grounds in winter ("dominance hypothesis"; Ketterson 1979; Ketterson and Nolan 1983), 2. intra-sexual competition favors individuals that arrive on the breeding grounds earliest, i.e., those that winter close by ("arrival time hypothesis"; Ketterson and Nolan 1983), and 3. differences in cold tolerance between the sexes allow the larger sex to survive harsher climates ("body size hypothesis"; Ketterson and Nolan 1976). Myers (1981) and Hines (1986) tested these hypotheses on scolopacids and tetraonins, respectively, and concluded that the arrival time hypothesis best explained sexual segregation of these groups. However, Ketterson and Nolan (1983) reviewed the above hypotheses both for dark-eyed juncos (*Junco hyemalis hyemalis*) and bird populations in general, and concluded that no single-factor hypothesis could adequately explain sexual segregation. Instead, they applied a multi-factor hypothesis ("threshold hypothesis"), first tested by Baker (1978), to birds. According to this hypothesis, birds migrate only when a migration threshold has been exceeded; i.e., when the advantages of remaining near the breeding grounds are outweighed by the advantages of leaving (Ketterson and Nolan 1983). Segregation of the sexes occurs when males and females have different migration thresholds.

Male willow ptarmigan (Lagopus lagopus) remain with their mates and chicks throughout brood rearing (Wittenberger 1978), but after brood break-up in September the sex and age classes segregate (Mossop 1987). Most adult males remain in subalpine habitat, whereas females and the majority of juveniles move to the boreal forest (Weeden 1964; Irving et al. 1967; Höhn 1984). According to the arrival time hypothesis, males remain close to their territories throughout the year because they invest heavily in territorial defence, whereas females, which invest less in defence, can move farther to take advantage of better food and/or cover (Hines 1986). However, Mossop (1987) observed that willow ptarmigan at Chilkat Pass, B.C. did not move from the breeding area until February, and in a year with little snow most females remained throughout the winter near the breeding grounds. Hence, the extent of migration and segregation of the sexes may vary annually. This suggests that the migration threshold hypothesis may apply to winter movements of willow ptarmigan. To test if this is the case, the timing and proximate causes of movements by ptarmigan must be known.

To date, studies that documented movements of ptarmigan outside the breeding season used either counts or band recoveries from hunters (Weeden 1964; Myrberget 1976; Gardarsson 1987; Mossop 1987). These methods can provide an estimate of direction and distance of ptarmigan movements, but as ptarmigan move farther from their breeding grounds, the chance of finding marked birds becomes exponentially smaller, resulting in a bias towards short-distance movements (see Greenwood and Harvey 1982). Therefore, they are not a good useful qualitative measure. Moreover, it is difficult to examine the timing and causes of winter movements with these methods. With the advent of radio telemetry, it became possible to follow individual ptarmigan from one breeding season to the next. I equipped adult willow ptarmigan at Chilkat Pass, B.C. with radio transmitters during the summers of 1987 and 1988. I followed these birds throughout the autumn and winter of 1987-88 and 1988-89 to document: 1) the timing and extent of movements by ptarmigan over these two seasons, 2) the factors influencing movements of ptarmigan during autumn and winter, 3) the degree of segregation of male and female ptarmigan at Chilkat Pass, and 4) whether the migration threshold hypothesis applies to winter movements of willow ptarmigan.

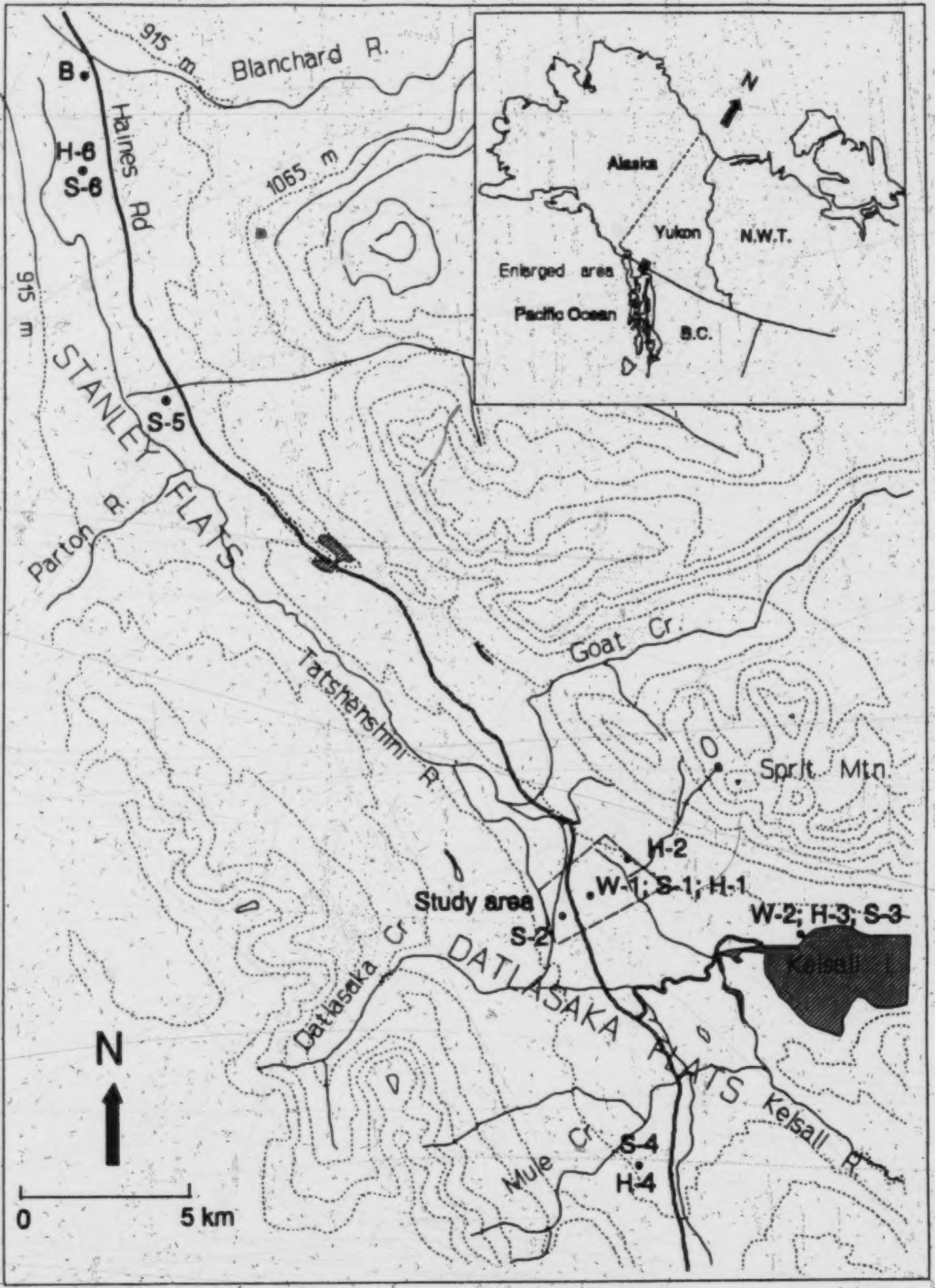
2.2 STUDY AREA

2.2.1 Topography

I conducted this study from September-March 1987-88 and August-April 1988-89 at Chilkat Pass in northwestern British Columbia (59°50'N., 136°35'W.; Appendix 1). Ptarmigan breed in subalpine habitat dominated by 1.5m high willow (Salix spp.) and dwarf birch (Betula glandulosa) (Weeden 1960). On the Pacific side the Chilkat Pass descends abruptly into a narrow valley covered by coastal forest, with a dense cover of willow and alder (Alnus spp.) at higher elevations (Weeden 1959). To the north, the Pass descends into an open-canopy white spruce (Picea glauca) forest, with scattered willow and birch in the understorey. The ground at Chilkat Pass is usually snow-covered between October and May. During most winters snow depth reaches approximately 1-1.5m.

Willow ptarmigan have been studied since 1979 on a 4.5km² site located in the northeastern corner of Datlasaka Flats and on the lower slopes of Sprit Mountain (Figure 2-1; "study area"). The site has been divided into 100x100m squares by means of permanent grid stakes (Hannon 1983).

Figure 2-1 Map of study area at Chilkat Pass, B.C. S=Snow measurement sites, H=Habitat measurement sites, W=Wind-run measurement sites, B=Barometric pressure measurement site. Ptarmigan were banded inside the area outlined by the square.


915 m
Blanchard R.
B
H-6
S-6
Haines Rd
1065 m
915 m
STANLEY FLATS
S-5
Parton R.
Tatshenshini R.
Goat Cr.
Spirit Mtn.
H-2
W-1; S-1; H-1
Study area
S-2
W-2; H-3; S-3
Kelsall L.
Datlasaka Cr.
DATLASAKA FLATS
Kelsall R.
Mule Cr.
S-4
H-4
N
0
5 km
N
Alaska
Yukon
N.W.T.
Enlarged area
Pacific Ocean
B.C.

2.3 METHODS

2.3.1 Capture, marking, and radiotelemetry

Ptarmigan were captured by driving them into gill nets strung along shrubs, or by noosing them with collapsible noosing poles (Hannon 1983). Each bird was marked with a unique combination of an aluminum and three plastic color bands, following the procedure outlined by Hannon (1983). Sexes were distinguished on the basis of differences in plumage and voice, and age was estimated by comparing pigmentation on the eighth and ninth primary (Bergerud et al. 1963).

In July of 1987, I equipped nine territorial males and nine resident females with 18g, 3.5V, two-stage radio transmitters (Austec, Edmonton, Alta), which had a life expectancy of up to five months. They were attached to the bird using a necklace made of harness wire (Schieck 1988; Appendix 2). I tracked these birds from September 15 until batteries expired in November. In July of 1988, I equipped 23 territorial males and 26 resident females with transmitters with a battery life of one year (Biotrack, Wareham, Dorset, UK; Appendix 2). They were attached with a necklace of harness wire (Schieck 1988) or soft cord (Kenward 1987). Weight of these transmitters ranged between 15 and 21g. I tracked the radio-tagged birds from August 1 until April 1989. Additional data were available from 1985, when J.O. Schieck followed movements of 16 radio-tagged females from April until September 1 (Schieck 1988).

I attempted to visually locate each radio-collared bird once per week, using hand-held Yagi antennas. However, during winter this was often not feasible, as many birds were inaccessible. When birds were observed I recorded their location and height of the vegetation (in dm above the snow) within a 10m radius of each bird. In 1988-89 I also located radio-tagged ptarmigan by triangulation using a truck-mounted removable null-dipole antenna, modified after Hallberg et al. (1974; Appendix 2). I tried to triangulate the position of each tagged bird once a week, and more often if time and weather permitted. In 1988-89 I conducted four aerial surveys between January and March to locate lost and inaccessible birds. The surveys covered all valleys within a 50-100km radius to the south, east, northwest, and north of Datlasaka Flats.

2.3.2 Home ranges

The exact size of the territory was not known for each bird in this study, as it can only be calculated accurately when boundary disputes with neighbours are recorded during spring territoriality (Hannon 1983). Therefore, in all calculations I used their breeding home ranges, defined as the area used between May 5 and June 20. During this period both males and females were on their territories. I used the arithmetic mean of these locations, converted to Universe Transverse Mercator (UTM) coordinates, as the centre point of the territory to calculate the distance tagged adults moved from their territories in autumn and winter. Although more sophisticated methods exist for calculating centre points of activity (Kenward 1987), the size of the error in conversion from grid to UTM coordinates (Appendix 2) in relation to the home range size of ptarmigan did not justify their use. In autumn I considered a bird within its home range if it was sighted within 100m of its breeding home range.

2.3.3 Winter molt

During my first field season I observed that during September and October most birds moved to different locations. At this time willow ptarmigan molt from their autumn plumage, which they attain in July, into a distinct white winter plumage (Salomonsen 1939). To determine if movements in September and October coincided with molt into winter plumage, I scored molting in 1988 by assigning percentages from 0-100 to the head, neck, and back separately, 0 being unmolted (brown), and 100 being completely white (see Hannon and Wingfield 1990). Molt was estimated to the nearest 10 percent. I added the three numbers to obtain a total molt score. I defined the location to which birds moved in late September as their molting area.

2.3.4 Autumn and winter periods

I divided each autumn and winter into six time periods of approximately 60 days each (except winter molt, which was 30 days). I based the periods on changes in migratory behavior. When I could not determine exactly when a bird changed its behavior (e.g., on what date it moved from its brood rearing area to winter molting area) I used the average date of all collared birds. The periods were defined as follows, with average dates for all birds in brackets: brood rearing, from Aug. 1 (start of the study) until the onset of winter molt (Sept. 23), winter molt, molt into winter plumage (Sept. 24-Oct. 23), autumn territoriality, from the time ptarmigan returned to their territories in October-November until they left in November-December (Oct. 24-Dec. 10), early winter movements, from the time ptarmigan left the breeding grounds until Jan. 31, late winter movements, from Feb. 1 until ptarmigan returned to their territories in spring, and transient spring territoriality, from the time ptarmigan first returned to their territories in spring until they settled permanently.

I defined the areas to which ptarmigan moved when they left the breeding grounds in November-December as their wintering grounds. Because many birds did not spend the entire winter in one location, I used the location in which each bird spent more than 50% of the winter as its winter location. The distance travelled to and from the wintering grounds was measured on a map along the most likely route taken, i.e., through the valleys rather than across mountain ranges.

2.3.5 Comparison of habitat between breeding and wintering areas

To compare habitat characteristics between the breeding and wintering areas, I set up six permanent grids in September of 1988 on which I measured change in vegetation cover and height over the winter (H-1-6 on Figure 2-1). Two sites were located on the intensive study area: one ("Haines Road", H-1) on the flood plain of Datlasaka Creek, and one ("Sprit Mountain", H-2) on the lower slopes of Sprit Mountain. Three sites were placed in nearby areas where males were found throughout winter 1987-88: "Kelsall Lake" (H-3) was located on the lower slopes of Mount Kelsall on the north shore of Kelsall Lake, "Mule Creek" (H-4) was located in an open spruce forest near the edge of subalpine habitat in the southwestern corner of Datlasaka Flats, and "Stanley Flats" (H-5) was situated on the central part of Stanley Flats, 500m south of the edge of an open spruce forest. The last site ("Forest Edge", H-6) was located at the edge of the open spruce forest north of Stanley Flats.

At each location I staked out 20 transect lines of 10m each (Figure 2-2). On the Haines Road and Sprit Mountain grids each transect was located 10m due north of permanent grid stakes. For the other four grids I chose a random starting point and line direction from an aerial photo, and marked out a permanent grid of 20 transects. I measured cover according to the line intercept method (Canfield 1941) along a 10m measuring tape on each transect. I expressed cover as a percentage of the line covered by vegetation. Because height of vegetation varied on the transect, I defined the average height of vegetation above snow level for each transect as the height

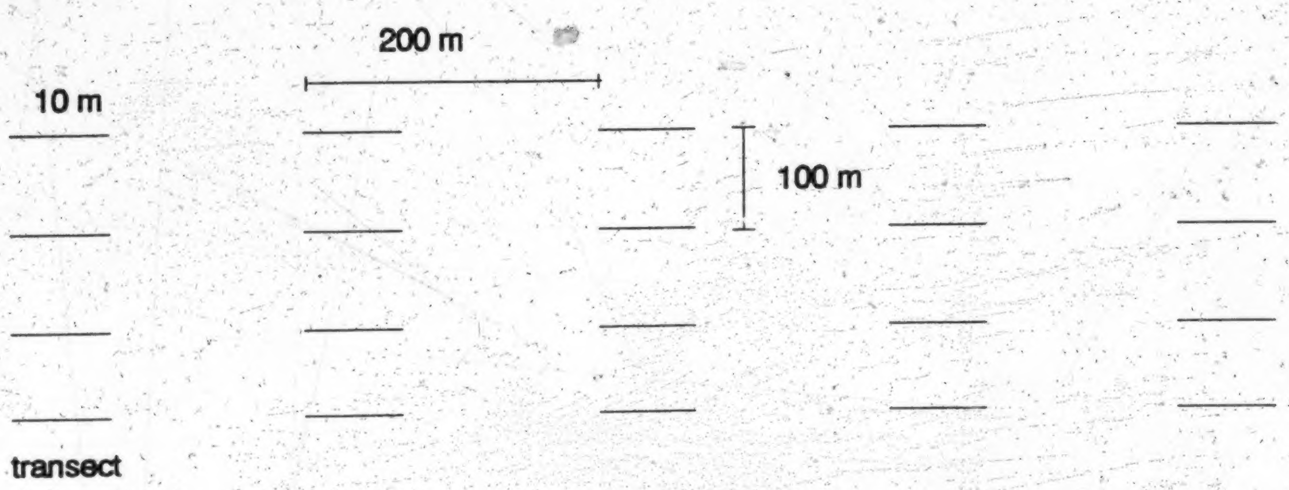

200 m
10 m
100 m
transect

Figure 2-2 Design of habitat measurement grids.

(rounded to the nearest 50cm) above which horizontal density was less than 10%. To measure density I divided a 2m x 0.5m board into 10 x 10cm squares. The board was placed upright at the stake marking each transect, and percentage of the squares covered by vegetation was counted from 10m away, at the end of the transect line (Nudds 1977).

2.3.6 Snow and weather

During the first season I recorded snow depth at permanent stakes on the intensive study site ("Haines Road", S-1 on Figure 2-1), at an accessible location where I expected males to winter ("Stanley Flats", S-5, see Mossop 1987), and among the trees at the edge of the boreal forest, where I expected females to winter ("Forest Edge", S-6). During the second season I added one more site on a part of the intensive study site where snow melted earlier in spring ("West Haines Road", S-2), and two sites in areas where I found males the previous winter ("Mule Creek", S-5, and "Kelsall Lake", S-6). All snow stations except West Haines Road were located within 200m of permanent habitat grids. At each of the six locations I randomly placed three 2m stakes in shrubs, and three in the open. I took snow depth measurements once every two weeks throughout each winter.

To compare wind speed between the breeding and wintering grounds I set up a wind-run meter at the study area in October 1988, which measured total accumulated wind in km at 2.5m above the ground/snow surface (Figure 2-1, W-1). An identical wind-run meter was set up on the north shore of Kelsall Lake, 5km to the east of the study area (Figure 2-1, W-2). I obtained an average wind speed by dividing the accumulated wind by the number of seconds between two readings.

I observed that both in autumn and spring ptarmigan left their territories during snow storms, and moved to protected locations (Sections 2.4.1.3, 2.4.2.1). Other authors have suggested that birds can predict bad weather through their sensitivity to changes in atmospheric pressure (Kreithen and Keeton 1974; J.C. Wingfield, pers. comm.). In 1988-89, I recorded atmospheric pressure at my residence at Blanchard River, 20km north of the study area (Figure 2-1, B), with a high precision barometer/altimeter (Thommen TX-21, accuracy ± 1 mbar). I calculated the intensity of low or high pressure condition by subtracting the relative atmospheric pressure for that altitude (913 mbar) from the absolute pressure.

2.3.7 Statistical analysis

When variables were distributed normally, I employed parametric statistics, otherwise I employed appropriate non-parametric statistics (Siegel 1956; Sokal and Rolph 1981). I used a Nonparametric Multiple Comparison by Simultaneous Test Procedure (STP-Test; Sokal and Rolph 1981) to test if differences were significant among multiple individual groups tested by non-parametric methods. Critical values for the STP-Test were corrected for ties (Sokal and Rolph 1981). In the analysis of two-way tables I used a G-Test, or a G-Randomization Test (G-Rand. Test) with 1000 iterations when one or more of the cells contained a value of less than 5 (Sokal and Rolph 1981). I considered differences significant when P values were less than 0.05.

2.4 RESULTS

In 1987-88 two (of nine) marked adult males and two (of nine) females, and in 1988-89 13 (of 23) males and 13 (of 26) females were killed through predation and hunting (Chapters 3 and 4). In addition I lost two radio-tagged males and two females in September 1987-88. In 1988-89 I lost four radio-tagged females after December (two of these birds returned the following spring with malfunctioning radios). I included these birds in the analyses until the time they were either killed or lost.

2.4.1 Timing and extent of movements on breeding grounds

Ptarmigan of both sexes remained on the breeding grounds until December of both years, but while on the breeding grounds they made short-distance movements which coincided with brood rearing, molt into winter plumage and autumn territoriality. In both years, the average distance ptarmigan were located from their summer territories was significantly different among these time periods (Table 2-1).

2.4.1.1 Brood rearing

In 1988 all males and all but one female were radio-tagged on their territories in the middle of July. Starting in late July/early August of 1988 the percentage of males and females remaining on their territories decreased gradually, until less than 20% remained on October 16 (Figure 2-3). In 1987 the percentage of males (n=4) and females (n=4) on their territories had dropped from 100% on July 18 to 75% and 0%, respectively, by September 15. The percentage of males further dropped to 50% on September 16, and to 25% on October 1. In 1985 the percentage of males (n=6) and females (n=8) on their territories dropped from 100% on July 20 to 67% and 50% respectively on August 28. Both in 1987 and 1988 all radio-tagged ptarmigan that left their territories moved uphill, but remained within 6km of their territories during brood rearing (Table 2-1). The direction of movement depended on the location of the territory: those birds with territories closer to the west side of the valley moved to the

Table 2-1 **Average distance (km) radio-collared willow ptarmigan were found from their summer territories during autumn**

a. 1987

Period[1]	Females					Males				
	Ave.	Med.	SE	Range	N	Ave.	Med.	SE	Range	N
Brood Rearing	1.98[2]	2.21	0.556	0.211- 3.400	5	1.09[2]	0.27	0.537	0.010-3.521	7
Winter Molt	4.05	4.20	1.101	1.088- 6.692	4	2.28	1.94	0.753	0.026-5.150	5
Fall Terr.	7.20	7.20	2.790	3.250-11.142	2	0.07	0.09	0.017	0.020-0.106	4

[1] See text for definition of time periods

[2] Values in column are significantly different at $P<0.01$ (Kruskal-Wallis Test).

b. 1988

Period[1]	Females					Males				
	Ave.	Med.	SE	Range	N	Ave.	Med.	SE	Range	N
Brood Rearing	1.18[2]	0.41	0.277	0.042-4.605	23	0.88[2]	0.21	0.293	0.001-5.658	22
Winter Molt	3.25	3.53	0.512	0.255-6.505	17	3.17	3.32	0.472	0.233-6.227	17
Fall Terr.	1.01	0.50	0.259	0.034-2.831	14	0.19	0.17	0.024	0.051-0.464	20

[1] See text for definition of time periods

[2] Values in column are significantly different at $P<0.001$ (Kruskal-Wallis Test).

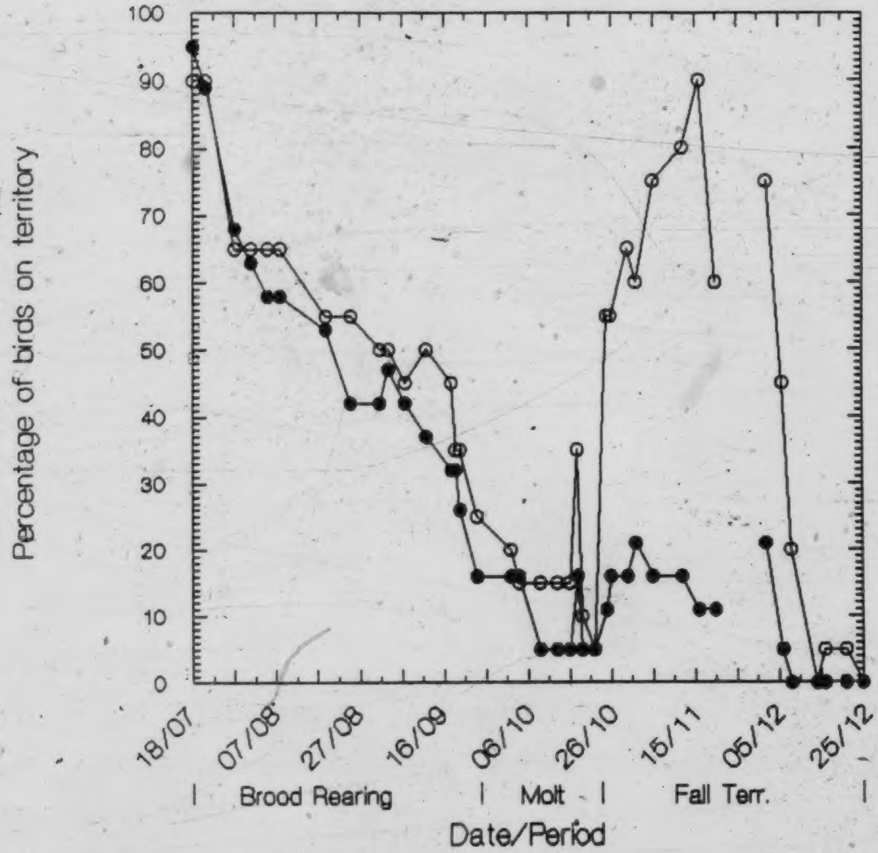


Figure 2-3 Percentage of radio-tagged male (O; n=20) and female (●; n=19) ptarmigan on their territories, July-December 1988. Only birds that were tracked throughout the entire period were included. I made no observations between November 21 and November 30.

western slopes, whereas those with territories on the east side moved uphill on the eastern slopes.

Neither sex nor reproductive success determined if a ptarmigan left its home range during brood rearing. Males did not remain on their territories more often than females (males on territory, 1985 and 1988 combined: 64.5% (20 of 31); females: 50% (16 of 32); G-Test, G=1.3, P=0.25). Eight of 19 females and 7 of 18 males with broods left their territories during the brood rearing period, whereas 3 of 8 females and 3 of 11 males without broods left their territories (G-Rand. Test; females: G=5.0, P=0.12; males: G=1.2, P=0.53). On the contrary, departure from territory in August appeared to be dictated by territory location. Most birds that occupied territories in the central, flat part of the study area left in August, whereas most birds that occupied territories along a nearby creek or on the hillside remained there throughout August (Figure 2-4). The central flat area from which birds left was on the course of an old river bed, which was clearly recognizable on air photos. Cover on the permanent habitat site on the old river bed (Haines Road) was significantly less (Figure 2-5), and average height of vegetation was significantly lower (Figure 2-6) than on the nearby hillside (Sprit Mountain). Thus, only birds occupying areas with less cover and lower vegetation may have left.

2.4.1.2 Winter molt

Starting in mid-September 1988 76% of 17 radio-tagged males and 59% of 17 females moved farther from their territories than they did during the brood rearing period. Both males and females were significantly farther from their territories during molt than during the brood rearing period (Table 2-1). Most birds remained within Datlasaka Flats, but 35% of males and 44% of 16 females moved to nearby side

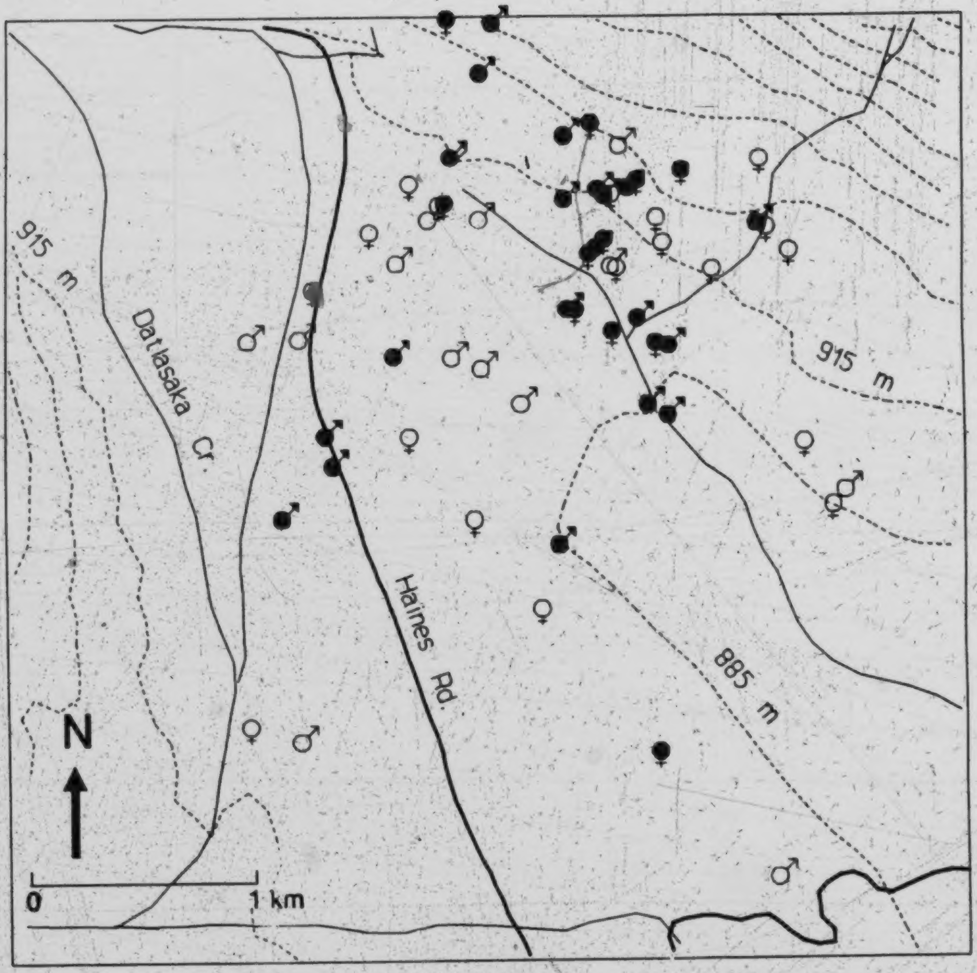

915 m
Datlasaka Cr.
Haines Rd.
915 m
885 m
N
0
1 km

Figure 2-4 Distribution of territories of radio-tagged males and females, respectively, known to be vacated (○) and occupied (●) from August 1 until September 1. Data from 1985 and 1988 combined. Data from 1987 omitted as fieldwork did not commence until 15/09.

Figure 2-5 Cover at permanent habitat sites on old riverbed (Haines Road), and hillside (Sprit Mountain) on breeding area, and in wintering areas (Mule Creek, Kelsall Lake, Stanley Flats, and Forest Edge), September 1988. n=20 for each site. Cover at sites with identical superscripts is significantly different at P=0.05 (STP-Test).

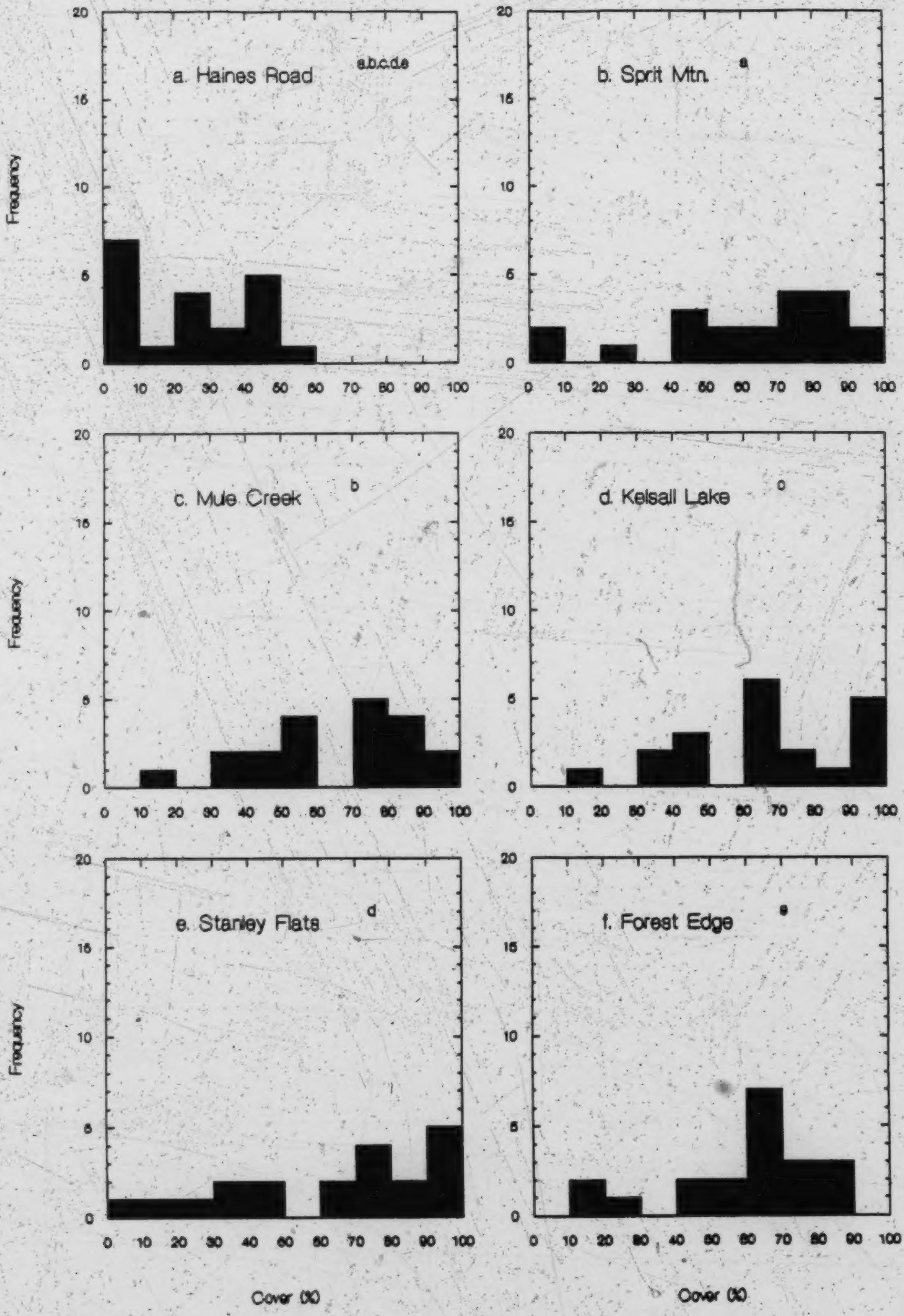
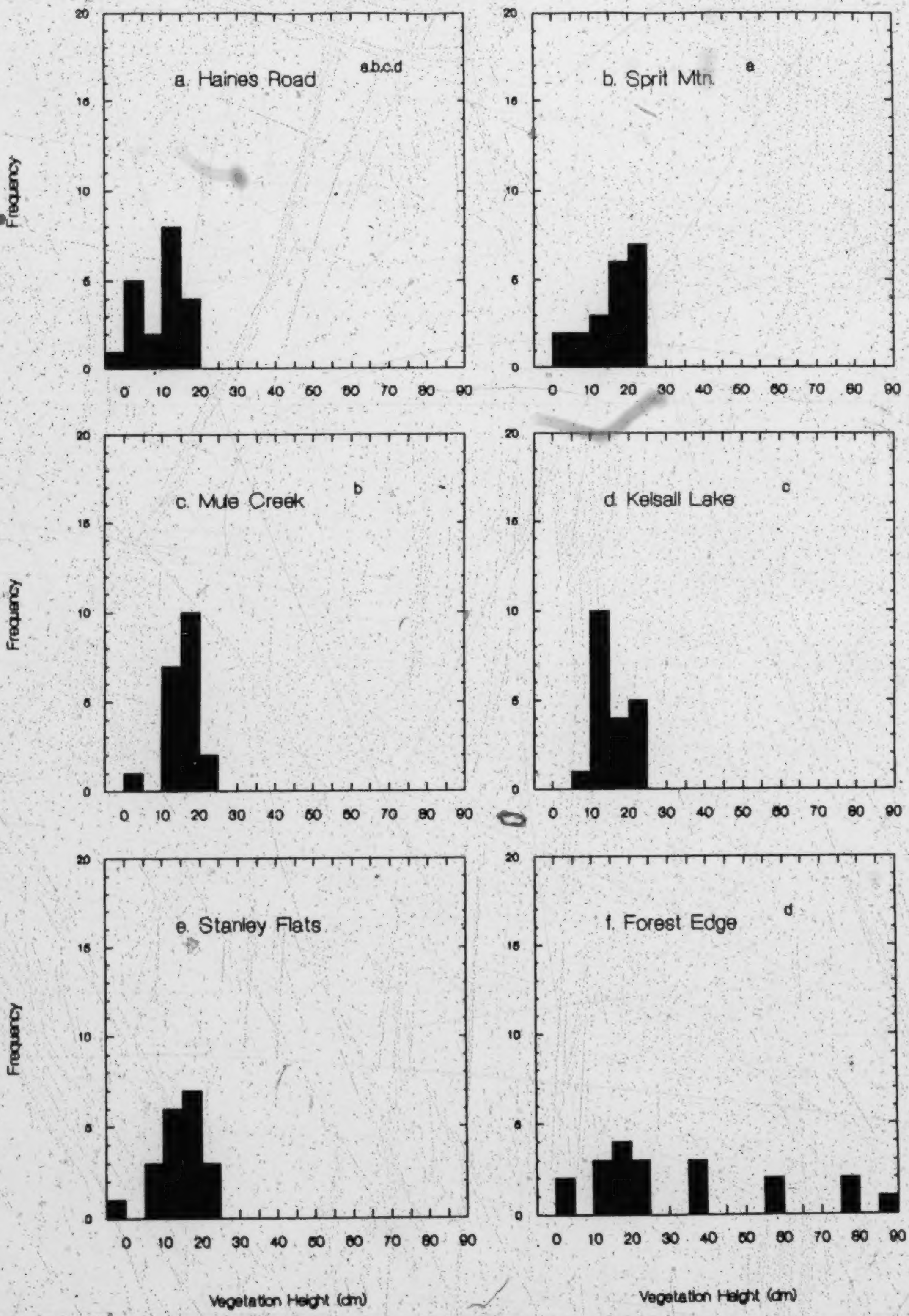

a. Haines Road
a,b,c,d,e
b. Sprit Mtn.
a
c. Mule Creek
b
d. Kelsall Lake
c
e. Stanley Flats
d
f. Forest Edge
e
Frequency
0
5
10
15
20
0
10
20
30
40
50
60
70
80
90
100
Cover (%)

Figure 2-6 Average vegetation height at permanent habitat sites on old riverbed (Haines Road), and hillside (Sprit Mountain) on breeding area, and in wintering areas (Mule Creek, Kelsall Lake, Stanley Flats, and Forest Edge), September 1988. n=20 for each site. Vegetation height at sites with identical superscripts is significantly different at P=0.05 (STP-Test).


a. Haines Road
a,b,c,d
b. Sprit Mtn.
e
c. Mule Creek
b
d. Kelsall Lake
c
e. Stanley Flats
f. Forest Edge
d
Frequency
0
5
10
15
20
0
10
20
30
40
50
60
70
80
90
Vegetation Height (dm)

valleys (Datlasaka Creek and Goat Creek; Figure 2-1). Moreover, 4 males and 1 female that I lost between mid-September and mid-October may have left Datlasaka Flats, as I searched the entire Flats. In 1987 20% of 5 males had left their territories by September 22, 40% by September 30, and 80% by October 7. Only one male did not leave its territory. The first all-white birds were seen on October 15 of that year, nine days before permanent snow cover. In both years movements were uphill from the brood rearing areas, and many birds moved well above the limit of vegetation into boulder fields. The timing of these movements preceded the onset of winter molt (Figure 2-7a). Salomonsen (1939) found that ptarmigan start to molt into winter plumage when the average temperature is 3-8 °C, and ends when temperatures are 9-11° lower. Temperatures at Chilkat Pass were approximately +5°C at the onset of the 1988 winter molt, and approximately -5°C at its termination (Figure 2-7b).

2.4.1.3 Fall territoriality

In 1988, 55% of 20 radio-tagged males and 16% of 19 tagged females returned to their territories on October 26 (Figure 2-8a). All males had returned by November 5, although at no time were all males on their territories simultaneously (Figure 2-8a). Moreover, some birds left their territories for short periods (see below). Fifty-three percent of 19 females returned to their territories, but they stayed a shorter period than males, and no more than 21% were on their territories simultaneously (Figure 2-8a). However, in 1988 females were significantly closer to their territories during autumn territoriality than during the molting period (Table 2-1b; STP-Test on birds seen in all 3 periods, females on and off territory combined; $U=138.0$, $P_{0.05}=134.6$, $P<0.05$). During both years, all of the females whose exact location was known remained within 10km of their territories (Table 2-1).

Figure 2-7 a. Percentage of radio-tagged adult male (O; n=17) and female (●; n=17) ptarmigan in winter molt area and average molt score ± SE (▴) of observed ptarmigan. I defined winter molt area as the area to which birds moved after the middle of September. Birds that did not leave their territory were not considered to be in a molting area.

b. average daily temperature (●) at the intensive study area, September-November 1988. First snow fall is indicated by an arrow.

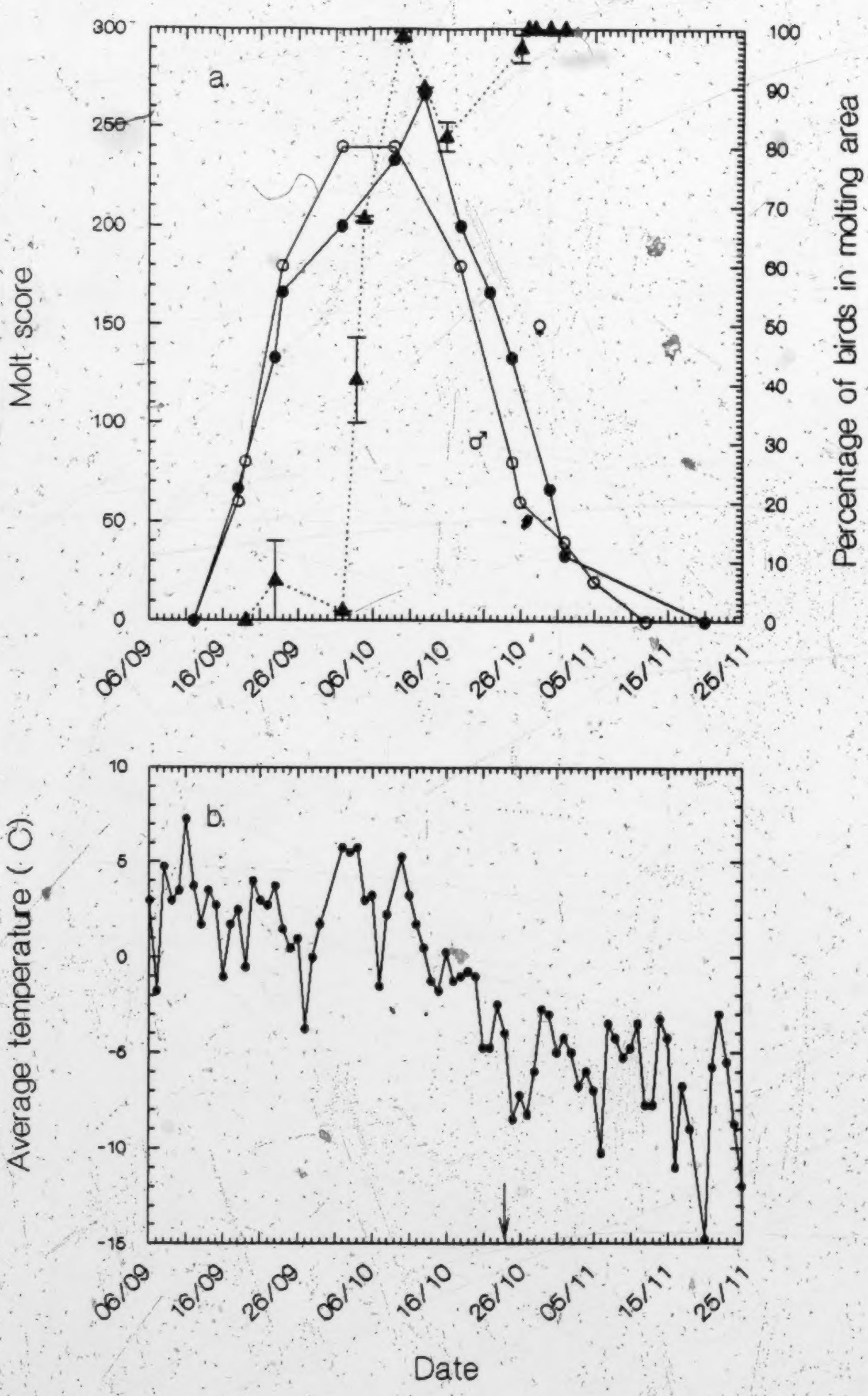
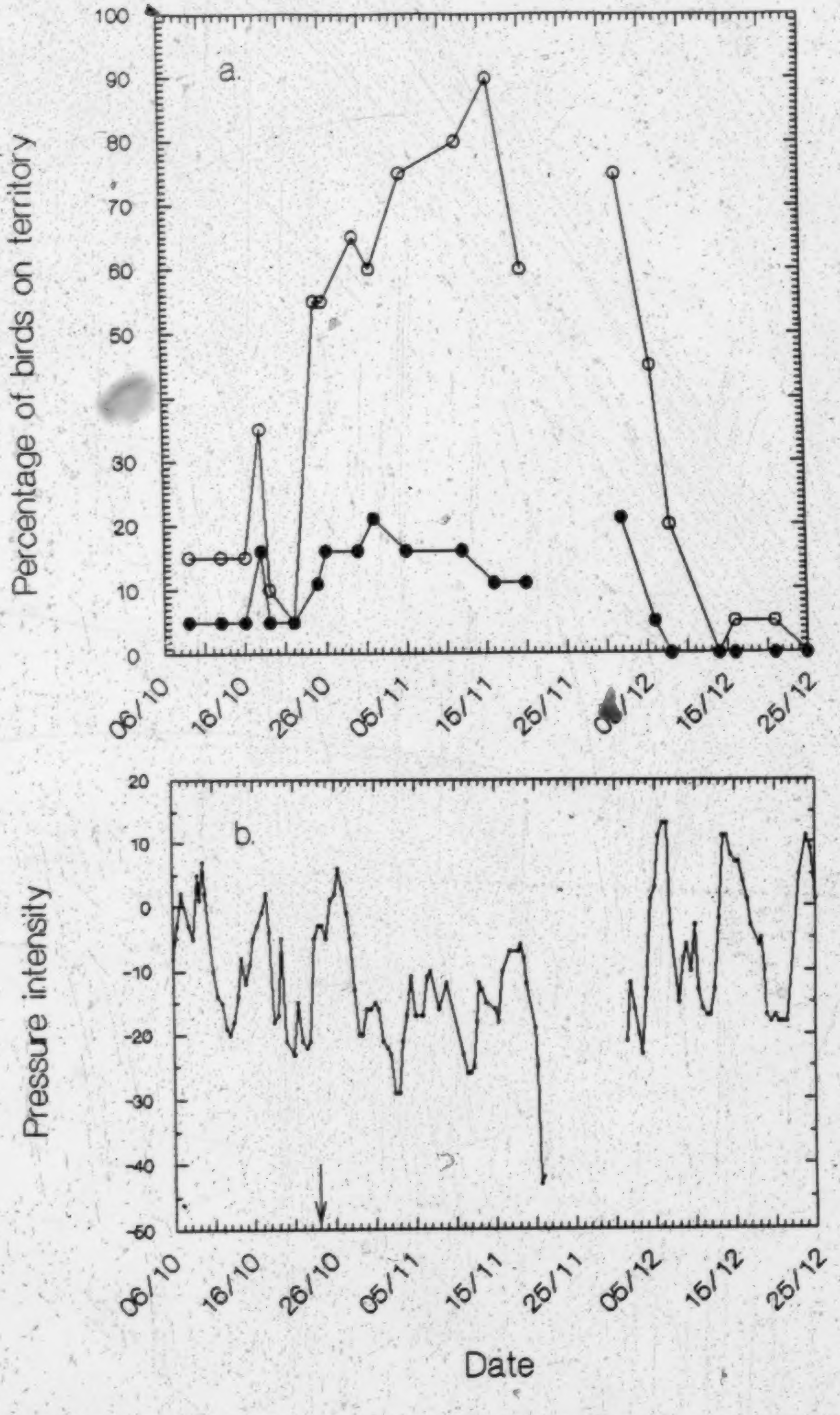

a.
Molt score
0
50
100
150
200
250
300
Percentage of birds in molting area
0
10
20
30
40
50
60
70
80
90
100
♀
♂
06/09
16/09
26/09
06/10
16/10
26/10
05/11
15/11
25/11
b.
Average temperature (°C)
10
5
0
-5
-10
-15
06/09
16/09
26/09
06/10
16/10
26/10
05/11
15/11
25/11
Date

Figure 2-8 a. Percentage of radio-tagged adult male (○; n=20) and female (●; n=19) ptarmigan on their territories, October-December 1988. I made no observations between November 21 and November 30.

b. Deviation of barometric pressure from relative barometric pressure (pressure intensity; mbar), October-December 1988. First snowfall is indicated by an arrow. I made no observations between November 21 and November 30.


a.
Percentage of birds on territory
100
90
80
70
60
50
30
20
10
0
06/10
16/10
26/10
05/11
15/11
25/11
05/12
15/12
25/12
b.
Pressure intensity
20
10
0
-10
-20
-30
-40
-50
06/10
16/10
26/10
05/11
15/11
25/11
05/12
15/12
25/12
Date

In 1987 all males had returned to their territories by November 8, but the exact date of return was not determined. I followed three radio-collared males at that time, one of which remained on his territory throughout autumn. Neither of the two tagged females returned to their territories in the autumn of that year, but one female whose transmitter had failed earlier, and one banded female without a radio were observed on their territories in November.

In both years, the supra-orbital combs became prominent on the males during autumn territoriality, although they appeared to be smaller than in spring. Male territorial calls were heard at dawn and dusk. Occasionally, a female territorial call was heard as well. In both years I observed many unbanded males along with banded males on territories on the study area, where during the breeding season approximately 95% of the breeding population was banded (Martin and Hannon 1987). I assumed that most unbanded birds were juveniles.

In 1988 the return of ptarmigan to their territories appeared to coincide with the first snowfall on the breeding grounds (Figure 2-8a). The first radio-tagged birds returned to their territories on October 18, when the lower limit of snow was approximately 100m above most territories. Although a snowfall for the entire area had been forecast, no snow fell, and all birds left again on October 19, prior to a large storm (Figure 2-8b). By October 24 all territories were covered with 1-5 cm of snow. Birds returned to their territories between October 23 and 26 (Figure 2-8a). In 1987 all territories were also covered with 1-5 cm of snow on October 24, but I could not determine if any birds returned to their territories immediately afterwards.

Between November 16 and 20, 1988 several birds of both sexes left their territories, but half the males and two of the females that left had returned by December 2 (Figure 2-8a). The temporary departures from territory in October and

November coincided with decreasing atmospheric pressure intensity (Figure 2-8b). However, not all storms were preceded by a sharp decrease in pressure. Nor did all declines in pressure forewarn a storm. Therefore, movements by ptarmigan off their territories were not influenced solely by changes in barometric pressure.

2.4.2 Movements from breeding grounds

In 1988 males moved to their wintering grounds significantly later than females (females: $\bar{x}$= Nov. 20; sd=10.6 days; n=14; males: $\bar{x}$=Dec. 5; sd=7.02 d.; n=20; t=4.3; $P<0.001$). By December 14, 1988 all radio-tagged ptarmigan had left their territories, and started moving towards their wintering grounds, although two males returned to their territories in the third week of December (Figure 2-8a). In 1987 all ptarmigan also left their territories in the second week of December. On December 10, 1987 I observed a flock of approximately 200 birds on the breeding grounds, and on December 15, after a three-day snowstorm, all ptarmigan had left. Ptarmigan wintering farther from the breeding grounds could be expected to leave their territories earlier than those wintering nearby. However, the departure date from the breeding grounds was not correlated with the distance ptarmigan of either sex moved to their wintering grounds (Spearman rank correlation; females: r_s= 0.08, n=13, $P>0.05$; males: r_s= -0.10, n=20, $P>0.05$).

In late December cover and height of vegetation above the snow was significantly heterogeneous among permanent habitat sites (H=46.0, df=5, $P<0.001$). The habitat sites on the breeding grounds (Haines Road and Sprit Mountain) had significantly less vegetation cover (Figure 2-9), and average height of vegetation was significantly lower (Figure 2-10) than alpine wintering areas (Mule Creek, Kelsall Lake, Stanley Flats), or at the edge of the boreal forest (Forest Edge). In September

Figure 2-9 Cover on the breeding area (Haines Road and Sprit Mountain), and in wintering areas (Mule Creek, and Kelsall Lake, Stanley Flats, and Forest Edge), December 1988. n=20 for each site. Cover at sites with identical superscripts is significantly different at P=0.05 (STP-Test).

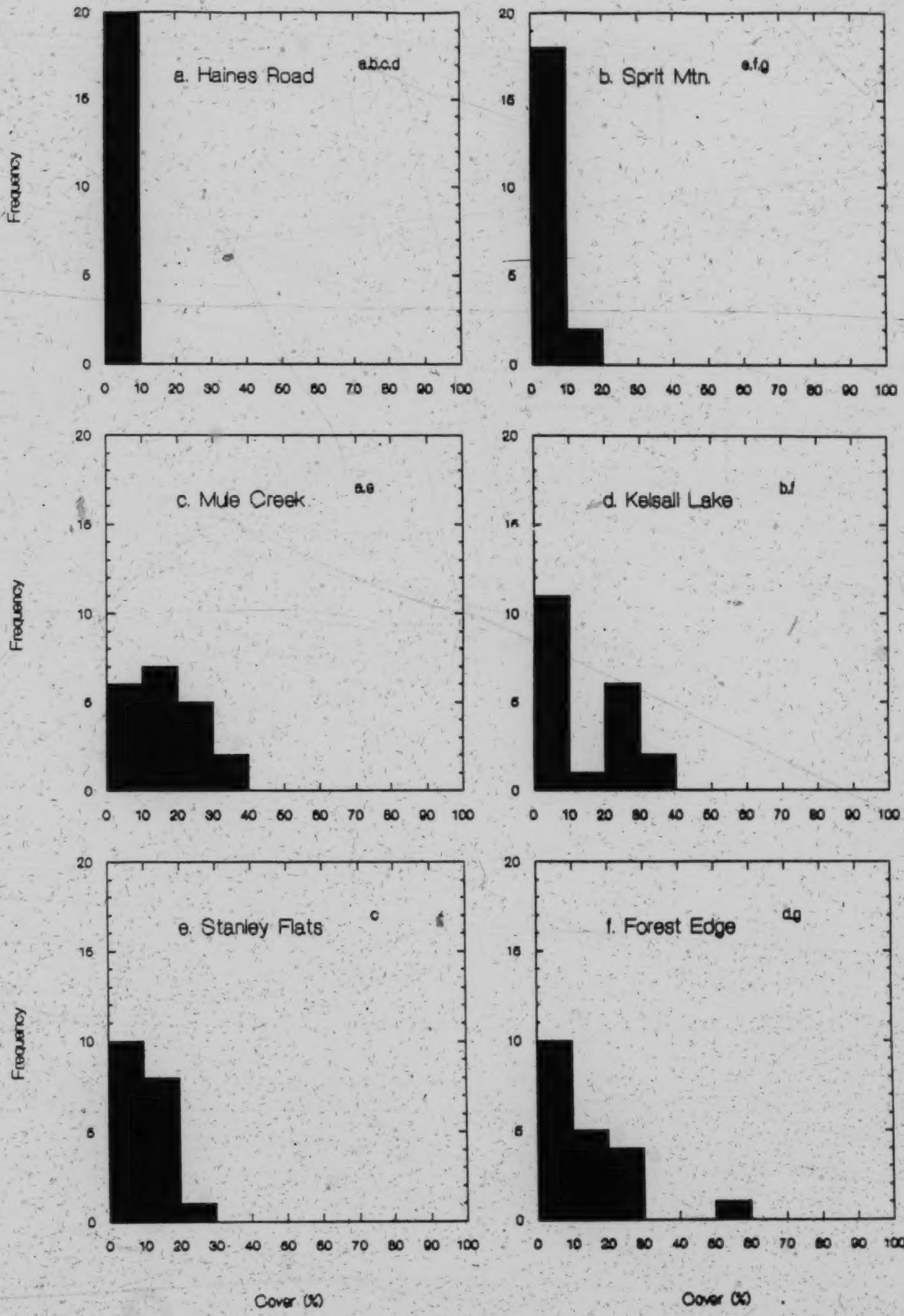
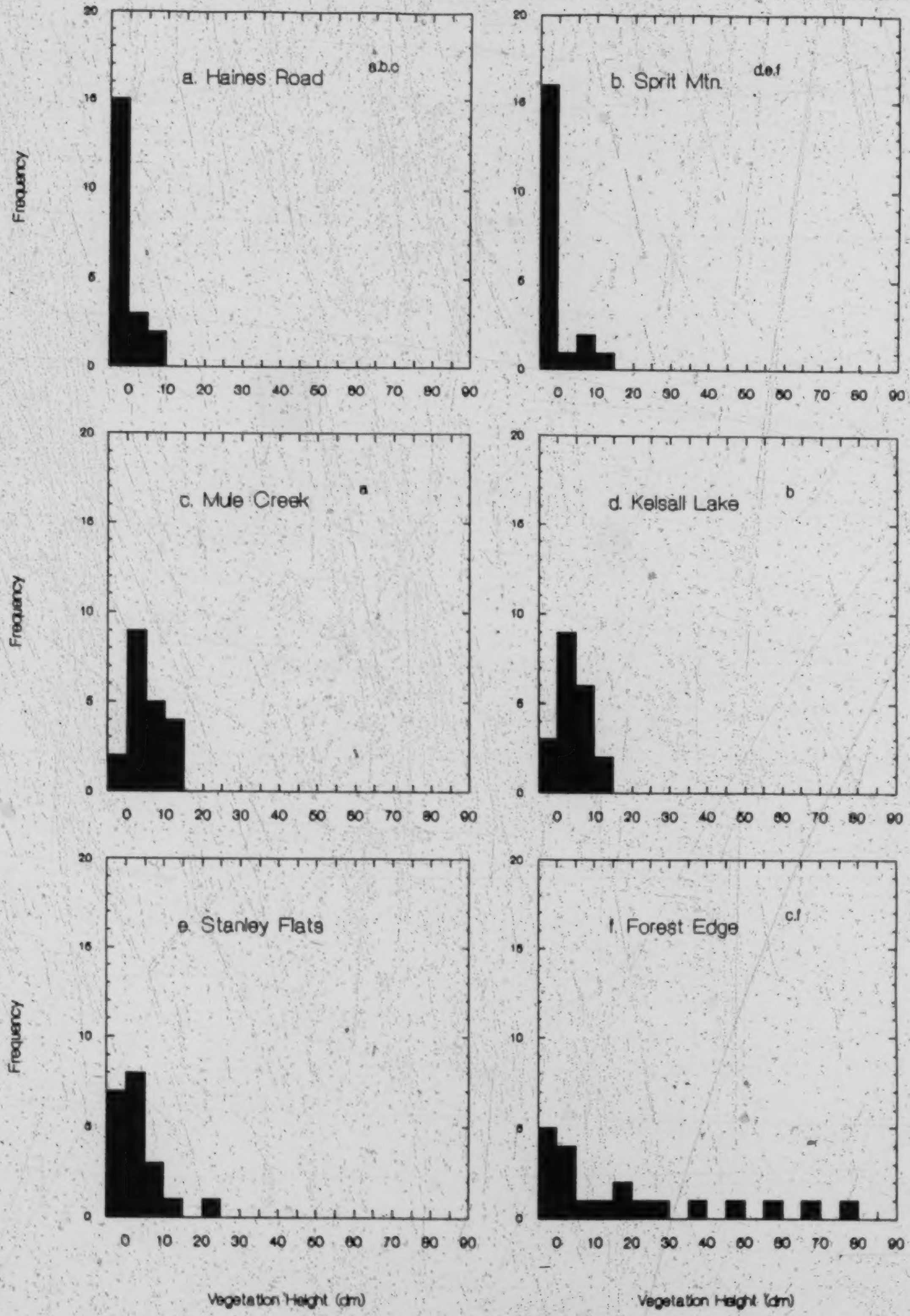

a. Haines Road
a,b,c,d
b. Sprit Mtn.
a,f,g
c. Mule Creek
a,e
d. Kelsall Lake
b,f
e. Stanley Flats
c
f. Forest Edge
d,g
Frequency
0
5
10
15
20
0
10
20
30
40
50
60
70
80
90
100
Cover (%)

Figure 2-10 Average vegetation height at permanent habitat sites on the breeding area (Haines Road and Sprit Mountain), and in wintering areas (Mule Creek, Kelsall Lake, Stanley Flats, and Forest Edge), December 1988. n=20 for each site. Vegetation height at sites with identical superscripts is significantly different at $P=0.05$ (STP-Test).


a. Haines Road
a.b.c
b. Sprit Mtn.
d.e.f
c. Mule Creek
a
d. Kelsall Lake
b
e. Stanley Flats
f. Forest Edge
c.f
Frequency
0
5
10
15
20
0
10
20
30
40
50
60
70
80
90
Vegetation Height (dm)

vegetation cover and average height of vegetation at Haines Road was significantly lower than at any of the other sites (Figure 2-5, 2-6), but cover and height of vegetation at Sprit Mountain was not. Hence, cover and height of vegetation was decreasing faster at Sprit Mountain than within the wintering areas.

Despite the difference in cover and height of vegetation among habitat sites in December, snow depth in that month was not significantly different among sites in either year (Figure 2-11; Kruskal Wallis Test; 1987: Open: H=4.73, P=0.09, df=2 ; shrubs: H=4.24, P=0.12, df=2 ; 1988: Open: H=9.69, P=0.08, df=5; shrubs: H=6.96, P=0.22, df=5). At all subalpine sites except Haines Road there was no difference between shrubs and open areas for most of the winter of 1988-89 (Figure 2-11a-e). The difference in snow depth between open areas and shrubs at Haines Road was related to high winds at that site: wind speed at Haines Road was much higher than at Kelsall Lake throughout autumn and winter 1988-89 (Figure 2-12; t-Test after Box-Cox transformation ($\lambda=1/3$); Haines Road: $\bar{x}=3.81$ m/s; Kelsall Lake: $\bar{x}=0.52$ m/s; t=10.6, df=1, P<0.001). Wind speeds at Mule Creek, the other part of Datlasaka Flats where many males spent the winter, appeared similar to those at Kelsall Lake. Thus the difference in vegetation cover and height between breeding and wintering grounds was at least partly caused by differences in wind speed.

One female moved to her wintering grounds 50km north of the breeding area in 8 days or less, but many ptarmigan did not move directly to the areas where they spent the majority of the winter. Eight of 20 males were known to have changed location during the course of the winter, as did four of 15 females. Birds that remained in subalpine habitat moved between Mule Creek and Kelsall Lake (10km), or from Datlasaka Flats to Stanley Flats (15km). Birds that had left Datlasaka Flats moved farther from the breeding grounds along the Tatshenshini River or its tributaries, or

Figure 2-11

a. Average snow depth ± s.d. in shrubs (●) and open areas (▲) on breeding grounds (Haines Road) during winter 1987-88 (...) and winter 1988-89 (——).

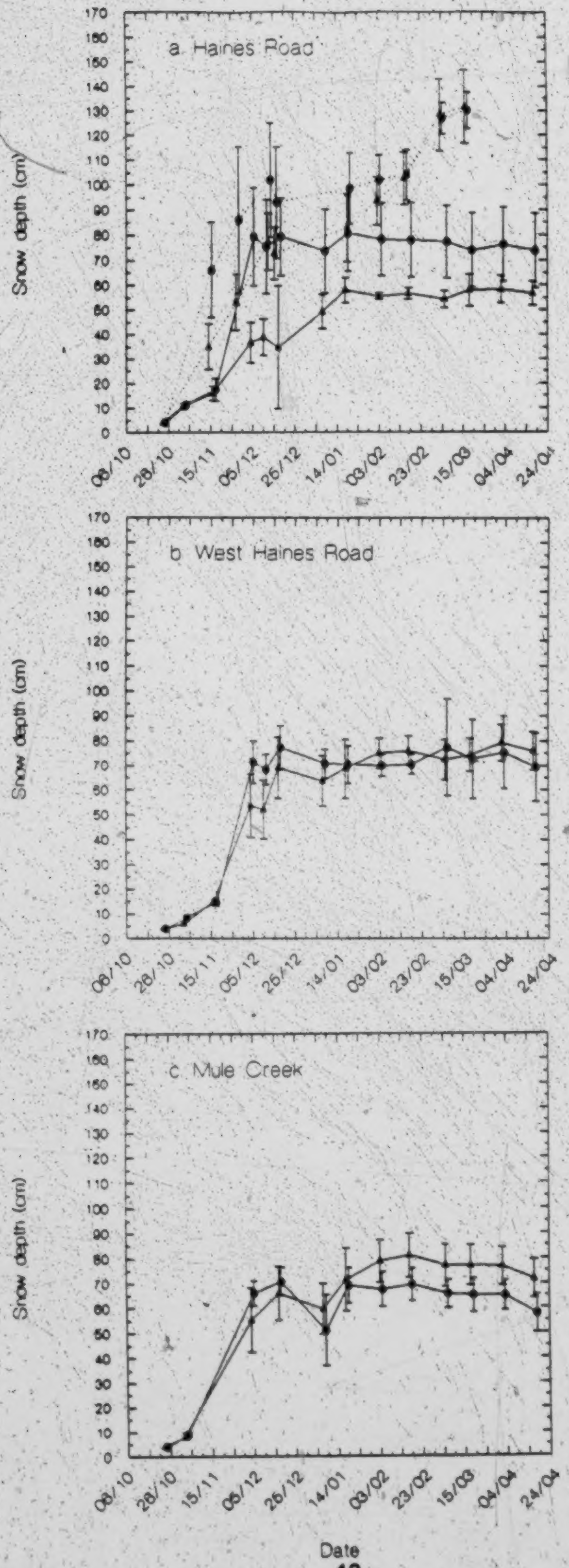
b. Average snow depth ± s.d. on western part of breeding grounds (West Haines Road) during winter 1988-89.

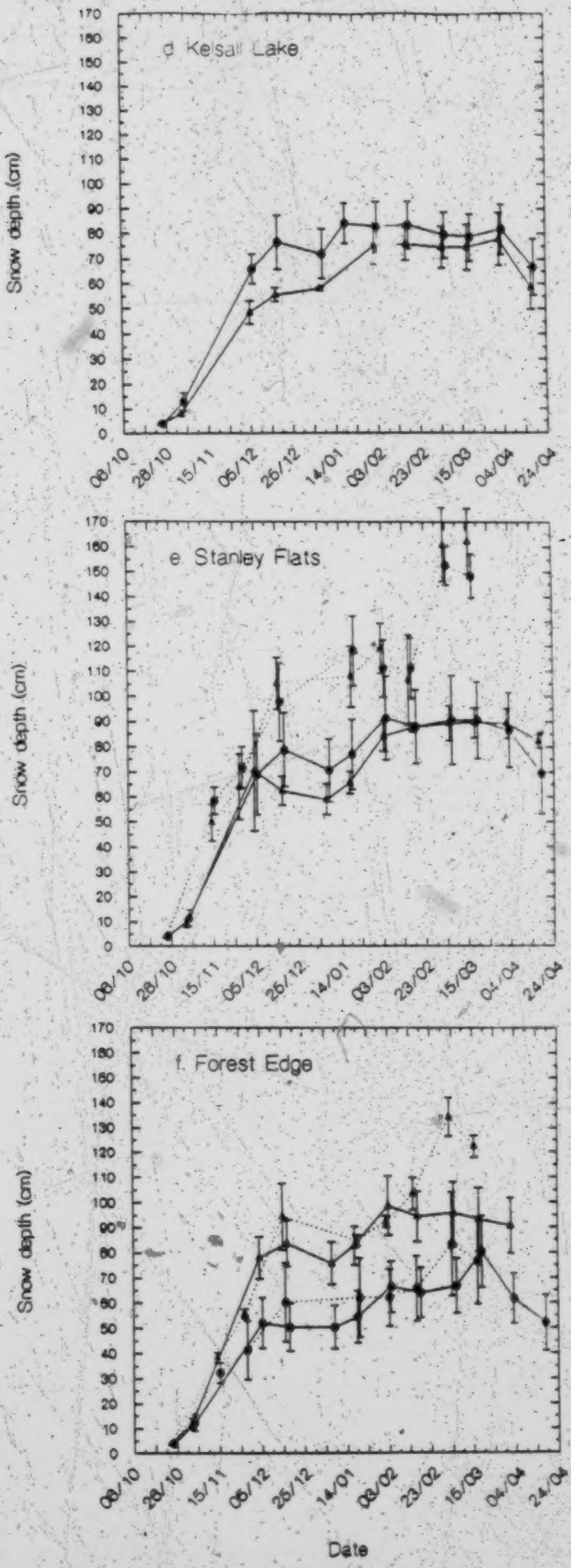
c. Average snow depth ± s.d. at Mule Creek during winter 1988-89.

d. Average snow depth ± s.d. at Kelsall Lake during winter 1988-89.

e. Average snow depth ± s.d. at Stanley Flats during winter 1987-88 and winter 1988-89.

f. Average snow depth ± s.d. at the edge of the boreal forest (Forest Edge) during winter 1987-88 and winter 1988-89.


a. Haines Road
b. West Haines Road
c. Mule Creek
Snow depth (cm)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
06/10
28/10
15/11
05/12
26/12
14/01
03/02
23/02
15/03
04/04
24/04
Date


d. Kelsall Lake
e. Stanley Flats
f. Forest Edge
Snow depth (cm)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
08/10
28/10
15/11
06/12
26/12
14/01
03/02
23/02
15/03
04/04
24/04
Date

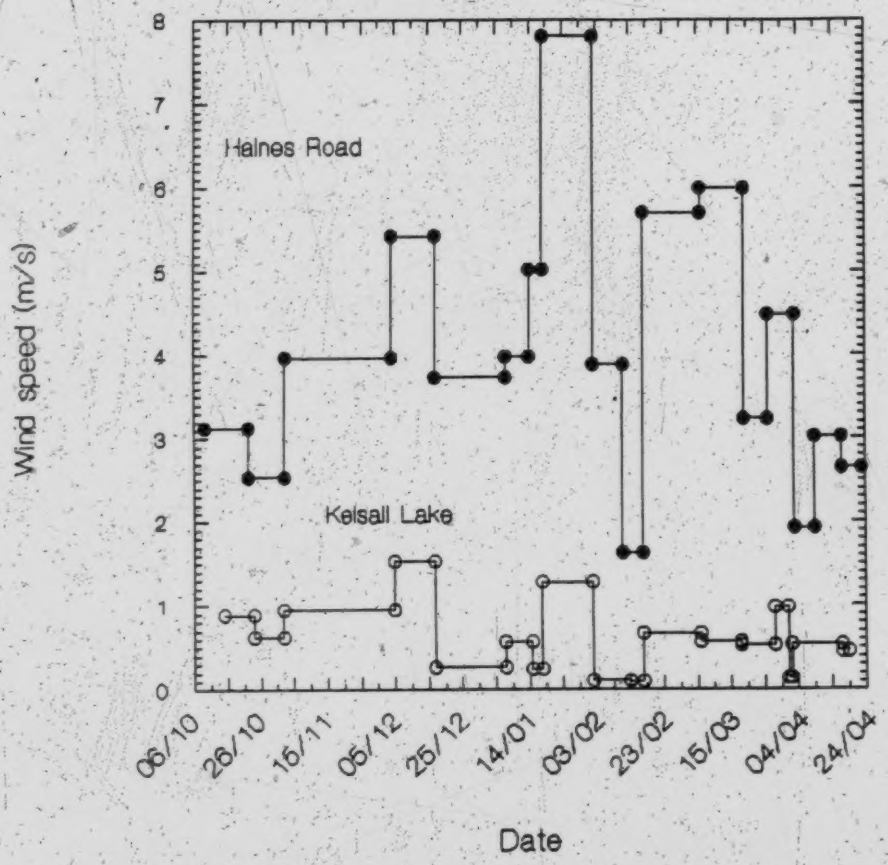


Figure 2-12 Average wind speed as measured by wind-run meters on breeding grounds (Haines Road; ●) and wintering grounds (Kelsall Lake; O), winter 1988-89.

along Kusawa Lake (Figure 2-13). However, several ptarmigan were lost during one of the two winter movement periods. When I excluded birds that were lost in one of the periods, neither males nor females were significantly farther from their territories in late winter than in early winter (Mann-Whitney U test; females: U=57.0, P=0.82; males: U=85.5, P=0.57). When data from early and late winter periods were combined, males moved significantly shorter distances than females (Table 2-2; Kolmogorov-Smirnov test; D=0.47, P=0.04). All birds that left Datlasaka Flats moved in a northerly or northeasterly direction (Figure 2-13). In those directions the edge of the boreal forest lies at approximately 20km from the breeding grounds. Thus, in 1988-89 20% of the adult males and 67% of adult females moved past the edge of the boreal forest during the winter. However, several males moved as far as females, and the longest recorded movement (90km) was made by a male.

2.4.2.1 Return to the breeding grounds

In 1989, radio-tagged males returned to their territories significantly earlier than females (males: $\bar{x}$= Mar. 21; sd=6.0 days; n=8; females: $\bar{x}$= Apr. 6; sd= 9.7 d.; n=8; t=3.9; P<0.01). The two males that returned to their territories in late December returned again in the second half of January, and stayed there the rest of the winter. The first of the remaining males returned to their territories on March 17 (Figure 2-14a). All males but one returned to their territories before the end of March. The date male ptarmigan returned to their territories was highly correlated with the distance they had to move from their wintering grounds (Spearman rank correlation; r_s= 0.95, n=8, P<0.01; males on territory since January excluded). The male that moved farthest and returned last was initially chased from his territory by unbanded males, but eventually reclaimed it. In 1988 the first males were sighted on their territories in the

Figure 2-13 Winter locations of radio-tagged adult male (○) and female (●) ptarmigan, winter 1988-89. When a bird was found in more than one area during the winter, the location where it spent most of the winter has been drawn.

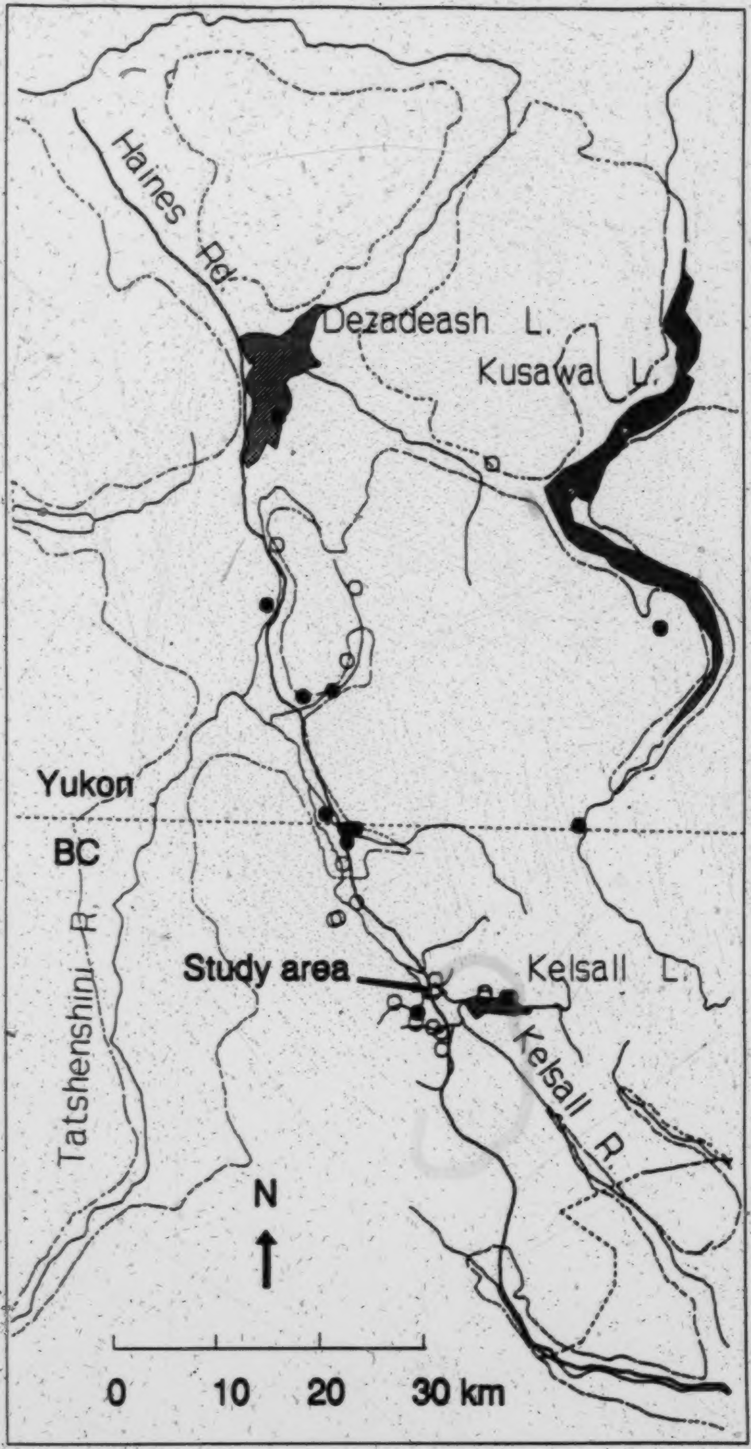

Haines Rd.
Dezadeash L.
Kusawa L.
Yukon
BC
Study area
Kelsall L.
Kelsall R.
Tatshenshini R.
N
0
10
20
30 km

Table 2-2 Comparison of maximum distances moved by radio-tagged adult males and females to their wintering areas, 1988.

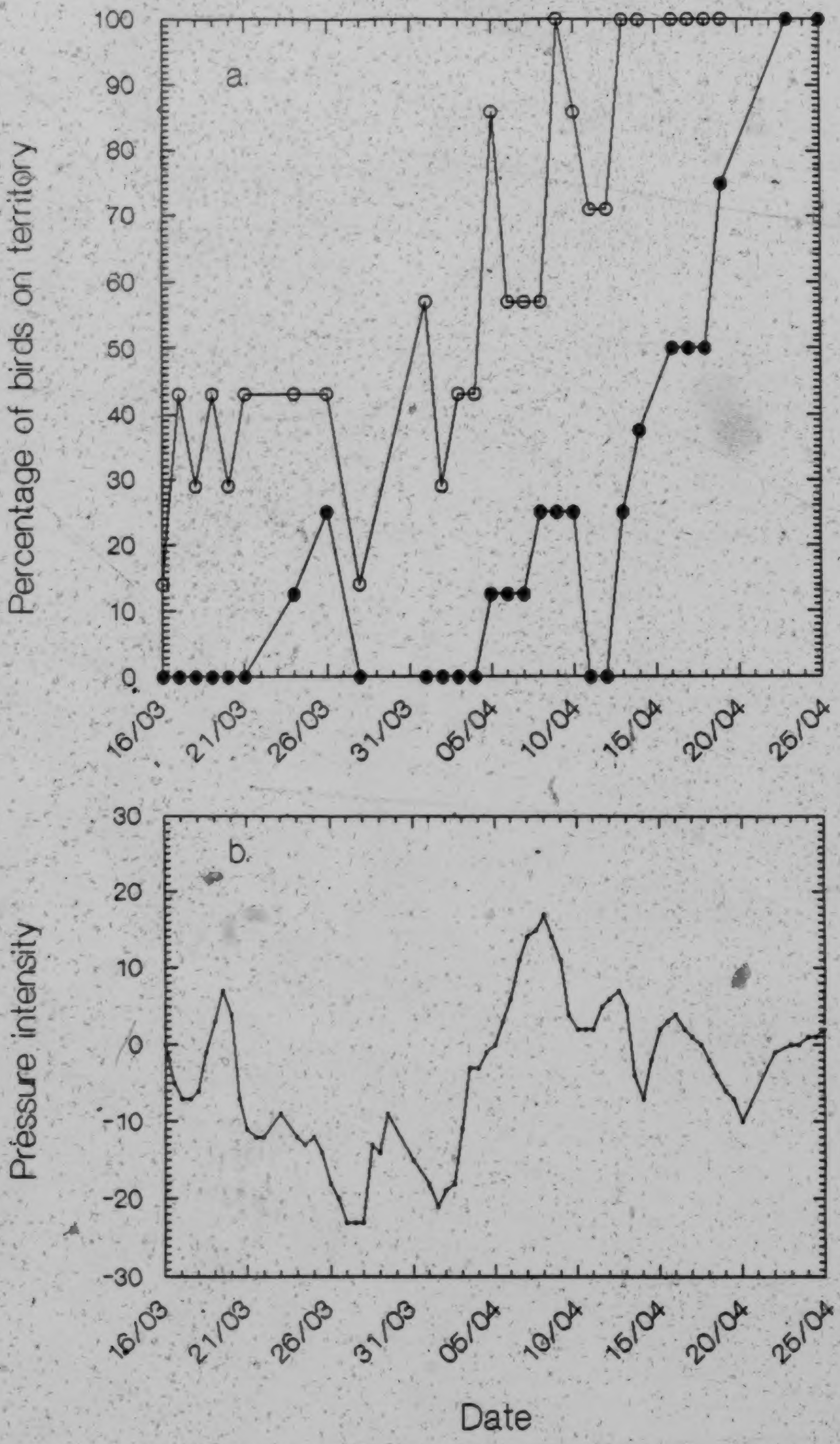
Distance from territory (km)	Males (n=20)		Females (n=15)	
	Percent	Cum. percent	Percent	Cum. percent
0-5[1]	25.0	25.0	6.7	6.7
5-10	35.0	60.0	26.7	33.3
10-15	10.0	70.0	0.0	33.3
15-20	10.0	80.0	0.0	33.3
20-25	0.0	80.0	26.7	59.9
40-45	5.0	85.0	20.0	79.9
50-55	5.0	90.0	6.7	86.6
55-60	5.0	95.0	6.7	93.3
85-90	5.0	100.0	6.7	100.0

[1] 0.001-5.000 km

Figure 2-14

a. Percentage of radio-tagged male (○; n=7) and female (●; n=8) ptarmigan on their territories, March-April 1989.

b. Deviation of barometric pressure from relative barometric pressure (pressure intensity; mbar), March-April 1989.


a.
Percentage of birds on territory
0
10
20
30
40
50
60
70
80
90
100
16/03
21/03
26/03
31/03
05/04
10/04
15/04
20/04
25/04
b.
Pressure intensity
30
20
10
0
-10
-20
-30
16/03
21/03
26/03
31/03
05/04
10/04
15/04
20/04
25/04
Date

same week as in 1989 (March 21). Yet, when male ptarmigan returned to their territories in March 1988, snow depth on the breeding grounds was nearly twice as great as when they returned in March 1989 (Figure 2-11a).

In March of 1989 cover and average height of vegetation were heterogeneous among habitat sites (cover: Figure 2-15; H=45.6, P<0.001, df=5; height: Figure 2-16; H=34.2, P<0.001, df=5). Cover at Haines Road was still significantly less than at the wintering grounds, whereas cover on Sprit Mountain was significantly less than at Mule Creek and at Kelsall Lake. Height of vegetation at Haines Road was significantly lower than at the wintering grounds, whereas height of vegetation at Sprit Mountain was significantly lower than at Mule Creek. Hence, the breeding grounds had less cover and lower vegetation than the wintering grounds when males returned.

In March 1988, snow depth in shrubs was significantly heterogeneous among sites (Figure 2-11; H=6.9, df=2, P=0.03), but not in open areas (H=4.5, df=2 P=0.11). On the other hand, when males returned in March 1989, snow depth was not significantly different among sites in either shrubs or in open areas (open: H=10.4, df=5 P=0.07; shrubs: H=4.4, df=1, P=0.50). Thus, the difference in cover and height of vegetation among sites was not caused by differences in snow depth.

If males tried to remain as close to their territory as possible, then the question arises why some males moved as far as females, especially because males that moved farther returned to their territories later. Males return to the same territory year after year (Schieck and Hannon 1989). Hence older males are more familiar with their territory, and may have an advantage over younger males when defending it. As a result, older males may be able to regain their old territory even if they arrive several days later than young males (Ketterson and Nolan 1983). There was a trend for males that moved to the forest to be older than males that stayed in the alpine (Alpine: ave.

Figure 2-15 Cover on the breeding area (Haines Road and Sprit Mountain), and in wintering areas (Mule Creek, Kelsall Lake, Stanley Flats, and Forest Edge), March 1989. n=20 for each site. Cover at sites with identical superscripts is significantly different at P=0.05 (STP-Test).

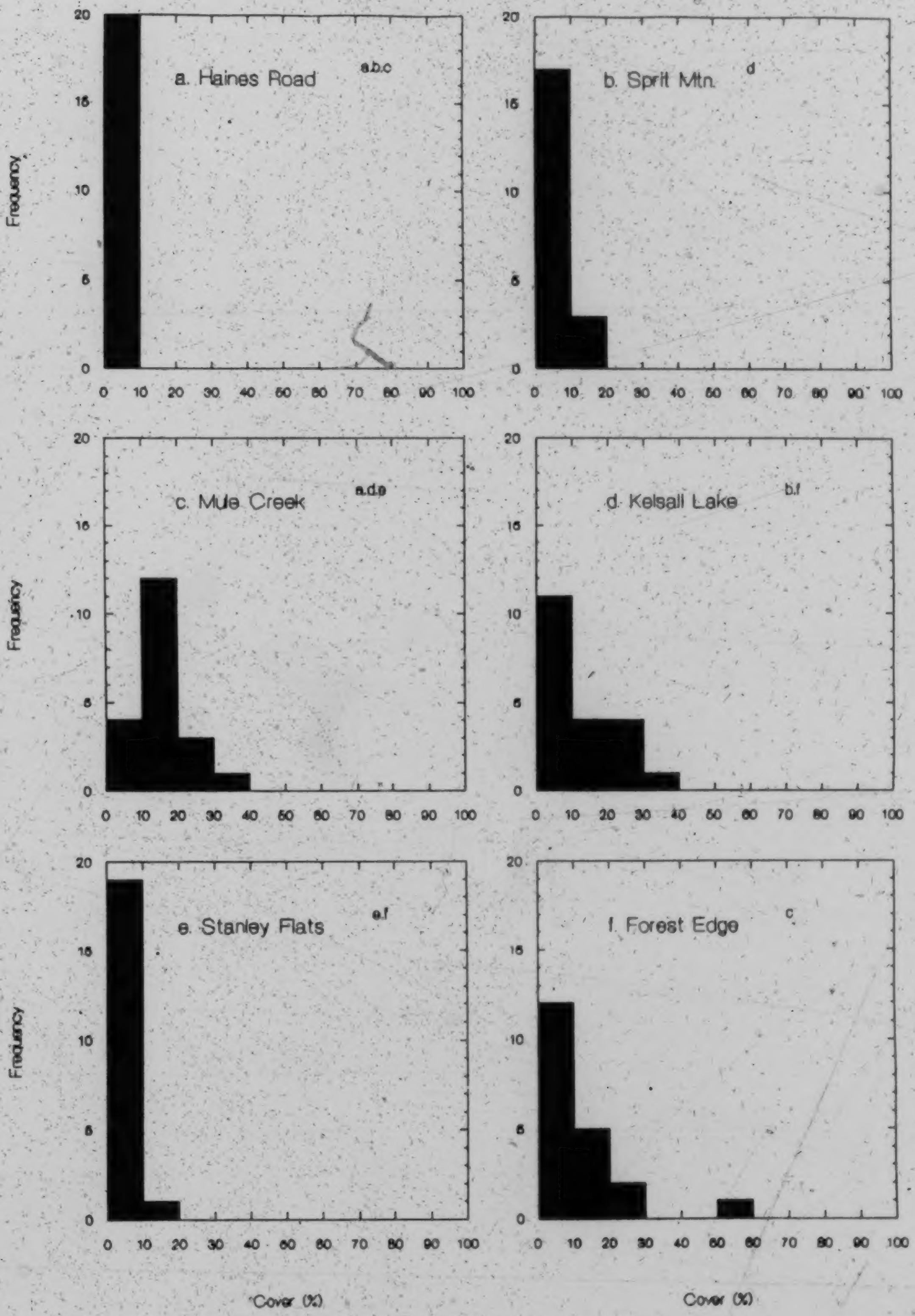
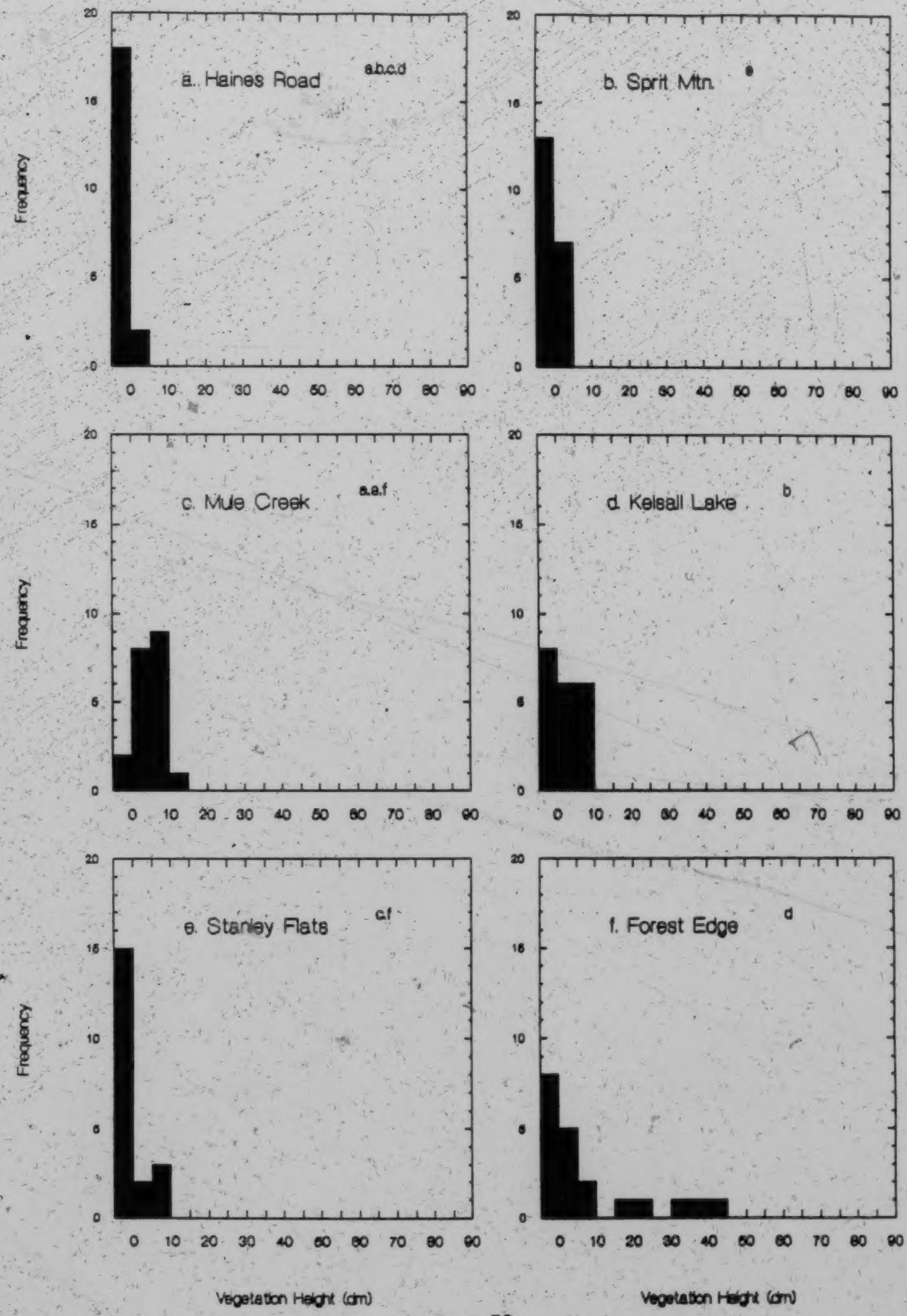

a. Haines Road
a,b,c
b. Sprit Mtn.
d
c. Mule Creek
a,d,e
d. Kelsall Lake
b,f
e. Stanley Flats
e,f
f. Forest Edge
c
Frequency
0
5
10
15
20
0
10
20
30
40
50
60
70
80
90
100
Cover (%)

Figure 2-16 Average vegetation height at permanent habitat sites on the breeding area (Haines Road and Sprit Mountain), and in wintering areas (Mule Creek, Kelsall Lake, Stanley Flats, and Forest Edge), March 1989. n=20 for each site. Vegetation height at sites with identical superscripts is significantly different at $P=0.05$ (STP-Test).


a. Haines Road
a.b.c.d
b. Sprit Mtn.
e
c. Mule Creek
a.e.f
d. Kelsall Lake
b
e. Stanley Flats
c.f
f. Forest Edge
d
Frequency
0
5
10
15
20
0
10
20
30
40
50
60
70
80
90
Vegetation Height (dm)

age=2.4 yr., sd=1.4, n=16; Forest: ave.=4.3yr, sd=2.9, n=4; t=1.86, $P<0.10$). However, there was no significant correlation between the distance males moved to their wintering grounds and their age (Spearman rank correlation; $r_s=0.26$, $P>0.05$).

In 1989, the first two females returned to their territories in late March, but left again after several days (Figure 2-14a). Most females did not arrive until the second week of April. The two females that returned early spent the winter nearby at Kelsall Lake. The other two females at Kelsall Lake also moved closer to the breeding grounds in late March, but were not seen on their territories. The two females that wintered along Kusawa Lake were the last birds to return to Datlasaka Flats, although other females settled later on their territories. The date females returned to their territories was correlated with the distance they had to move from their wintering grounds ($r_s=0.77$, n=8, $P<0.05$). In 1988 I did not record the return date of females. The age of females wintering near the breeding grounds was similar to that of females wintering farther away (Alpine: ave. age=1.8 yr., sd=1.0, n=4; Forest: ave.=2.0 yr, sd= 0.8, n=10; t=0.43, $P>0.5$).

After their return to the breeding grounds all females and all males but one left their territories and moved to protected locations at least once before settling permanently (Figure 2-14a). As in autumn, these departures from territory appeared to coincide with decreasing atmospheric pressure (Figure 2-14b). However, similar to the situation in autumn, changes in pressure did not accurately explain all movements of ptarmigan from their territories.

2.4.3 Height of vegetation near ptarmigan

In all periods of 1988-89, except for transient spring territoriality, average height of vegetation near ptarmigan was greater than 1m (Table 2-3). Ptarmigan that were off

Table 2-3 Vegetation height (dm) within 10m of ptarmigan at Chilkat Pass during winter 1988-89

Period[1]	On territory					Off territory				
	Ave.	Med.	SE	Range	N	Ave.	Med.	SE	Range	N
Brood Rearing	13.1	14.0	0.43	0-22	70	12.6	14.0	0.72	0-25	43
Winter Molt						11.0	11.0	1.15	0-20	18
Fall Terr.	12.7	12.5	0.36	1-20	66	12.0	10.0	0.80	6-17	17
Early Winter						13.4	15.0	1.11	0-30	31
Late Winter						13.1	8.0	2.29	0-50	25
Tr. Spr. Terr.	6.88	6.50	0.31	0-15	78	10.2	7.0	1.28	3-20	26

[1] See text for definition of time periods

their territories were found in vegetation of similar height throughout autumn and winter (Table 2-3, Kruskal Wallis Test; H=8.3, df=5, P=0.14). During all three periods that ptarmigan were found on their territories (brood rearing, autumn territoriality, and spring transient territoriality) birds on and off their territories were found in areas with similar height of vegetation (Mann-Whitney U Test; brood rearing: U=1545.5, P=0.79; autumn territoriality: U=684.5, P=0.11; spring transient territoriality: U=890.0, P=0.30). However, height of vegetation near ptarmigan on their territories was heterogeneous among periods (Table 2-3, H=97.8, df=2, P<0.001). Ptarmigan were found in tallest vegetation during brood rearing and lowest vegetation during spring territoriality. Thus, ptarmigan generally sought vegetation greater than 1m, but during transient spring territoriality tall vegetation was probably not available on the breeding grounds because males especially returned to their territories regardless of snow depth.

2.5 DISCUSSION

2.5.1 Timing and extent of movements on breeding grounds

Ptarmigan did not move to their wintering grounds directly after broods broke up, but remained on the breeding grounds until December. Between hatching of chicks and the departure of ptarmigan for their wintering grounds, they made distinctive movements within the breeding grounds which corresponded to brood rearing, winter molt, and autumn territoriality.

2.5.1.1 Brood rearing

After chicks hatched, birds occupying territories in areas with less cover and lower vegetation left their territories and moved uphill. Andersen et al. (1986) found that most willow ptarmigan in their study population moved uphill after chicks hatched. Rock ptarmigan (L. mutus) (Gelting 1937; Gardarsson and Moss 1970; Bossert 1980) and Colorado white-tailed ptarmigan (L. leucurus) (Braun 1971) also move uphill after chicks hatch. In some populations of rock ptarmigan the entire population moves uphill (Gelting 1937; Gardarsson and Moss 1970), whereas in others only part of the population moves (Bossert 1980). Colorado white-tailed ptarmigan move to rocky, often windswept areas at high elevations after the breeding season. They favor areas where snow starts to accumulate (Braun 1971). Gelting (1937), Braun (1971), and Andersen et al. (1986), suggested that ptarmigan moved to higher elevations after the breeding season because snow melted late there, delaying plant phenology. The nutritive value of plants decreases with age (van Soest 1983), and they concluded that therefore food quality at those elevations was higher than at the breeding grounds. Moreover, snow patches offer camouflage to white-tailed ptarmigan, which molt into winter plumage at that time (Braun 1971; See section 2.5.1.2). Variation in the extent of uphill movements and the proportion of the population that moves uphill is caused by variation in timing of snow melt (Andersen et al. 1986) and quality of the territories (see Mercer 1967). Variation in brood movements after the nesting period has been observed in other grouse well: Berry and Eng (1985) suggested that sage grouse (Centrocercus urophasianus) movements from the nest may be related to moisture conditions, and hence vegetation quality. Sopuck (1979) also suggested that food quality and availability caused female blue grouse (Dendrapagus obscurus) with broods to leave the nesting area.

On Brunette Island, off the coast of Newfoundland, willow ptarmigan broods moved shorter distances than in areas on Newfoundland (Mercer 1967). As dense vegetation was abundant on Brunette Island, in contrast to the other areas, Mercer

(1967) concluded that the brood movements decreased in areas with greater cover. However, he did not put forward predictions as to why ptarmigan searched for greater cover. Bergerud and Gratson (1987) suggested that in the first two weeks after hatch female grouse with broods select open, insect-rich habitats, but once chicks mature, females move to locations with denser cover to avoid detection by predators. I found ptarmigan both off and on their territories in dense cover during brood rearing. Mortality of adult ptarmigan was high during raptor migration in early September (Chapter 3). Hence, ptarmigan may attempt to reduce risk of predation by selecting areas with dense cover. At Chilkat Pass, variation in movements among ptarmigan may depend on food availability or quality on the territories as well as on availability of cover. As a result, only ptarmigan from territories lacking those components would move uphill.

2.5.1.2 Winter molt

Both male and female ptarmigan moved farther uphill from their territories starting in the middle of September, and five birds may even have left Datlasaka Flats. However, all males and half of the females returned to their territories later in the autumn. The movements in September preceded molt into winter plumage. Average temperatures at that time corresponded with Salomonsen's (1939) finding that winter molt starts when average temperature is 3-8°C and terminates when temperatures are 9-11°C lower. Hewson (1973) observed that the extent of winter molt in Scottish rock ptarmigan varied with mean winter temperatures. Ultimately, ptarmigan molt into white plumage because of snow cover. The first occurrence of permanent snow cover, however, is unpredictable. On the other hand, once average temperature drops below freezing, fallen snow is less likely to melt. Hence, the change in temperature from above to below freezing is a reliable cue to predict arrival of snow.

During winter molt many birds in my study moved well above the limit of vegetation onto boulder fields, where patches of snow were already present. Kristoffersen (in Myrberget 1976) noted that willow ptarmigan sought snow covered mountains or areas with light-colored Cladonia lichens during winter molt. Icelandic rock ptarmigan move to areas with snow during winter molt, and remain above the snow line (Gudmundsson 1960). Braun (1971) found white-tailed ptarmigan at high elevations during molt, and suggested that food quality at those elevations was better (see Section 2.5.1.1). Moreover, he suggested that snow patches and rocks offered camouflage for the molting birds. Thus, during the period in which ptarmigan molt into their winter plumage they may select areas which offer protection from predators because they are conspicuous, and (or) they may search for food high in nutritional value. To find suitable areas for molting, ptarmigan will clearly move considerable distances.

2.5.1.3 Autumn territoriality

In 1988 all radio-collared males and half of the females returned to their territories between late October and early December. During that time there was a resurgence of territorial defence, especially by males. Males appeared to return to their territories directly after the breeding area was snow covered. I saw no sign of males on their territories immediately after the first snowfall in 1987, but in that year I did not document the exact movements of radio-tagged birds. A similar resurgence in territorial activity has been observed in most willow (Mercer 1967, Pedersen et al. 1983) and rock ptarmigan (Watson 1965, Bossert 1980) populations. Braun and

Schmidt (1971) observed that white-tailed ptarmigan move downhill from their breeding grounds after the first snowstorms in September, but some birds return during calmer weather following the storms. These movements may also be linked to autumn territoriality.

The timing and extent of fall territoriality varies with local conditions. Harper (1953) and Bossert (1980) noted an increase in territorial calling of willow and rock ptarmigan, respectively, after first snowfall. On the other hand, autumn territoriality in Newfoundland willow ptarmigan (Mercer 1967) and Scottish red grouse (Jenkins et al. 1963) resumes as early as September, well before snowfall. Newfoundland ptarmigan probably do not molt into winter plumage until November (Salomonsen 1939), and red grouse do not molt into a white plumage at all (Salomonsen 1939). Hence, the difference in start of fall territoriality may be related to the timing of molt into winter plumage.

In both years of my study, territorial behavior ceased in December when all ptarmigan left the breeding grounds. In the absence of snow, or under mild winter conditions ptarmigan will defend their territories throughout the winter (e.g., Jenkins et al. 1963, Watson 1965), but most populations of ptarmigan are forced to leave their territories when food and cover becomes unavailable. As a result, territorial activity in autumn will be more pronounced among populations with sufficient food and cover, such as red grouse, and less obvious or absent when breeding grounds are snow covered early in autumn, as in white-tailed ptarmigan.

In contrast to my observations, Mossop (1987) concluded that ptarmigan at Chilkat Pass do not engage in territorial defence during autumn. He noted that more ptarmigan are present on their breeding areas in December than in November, but did not elaborate on the cause of the increase. Based on observations from Iceland, Norway, and Chilkat Pass, Bergerud et al. (1987) concluded that territorial behavior does not take place among ptarmigan during autumn, but they chose to ignore the clear evidence for such behavior that already existed then. Bergerud and Gratson (1987, p. 550) also assumed that juvenile male ptarmigan were not territorial in autumn because of conspicuousness between first snowfall and winter molt. However, they neglected to consider the period between winter molt and disappearance of food and cover under the snow. Moreover, as Watson and Moss (1987) pointed out, the brief period during which territorial activity takes place in autumn can easily be missed. Thus, it can now be safely assumed that ptarmigan defend their territories during autumn.

Lance (1978) observed that all surviving young male red grouse returned to their natal territory in autumn and competed with their father for space. This suggests that adult males return to their territories in autumn to defend them against their male offspring. Female ptarmigan display less during autumn than do males. Among rock ptarmigan, autumn territoriality also involves mainly males, but some females do call (Watson 1965; Bossert 1980). Martin and Hannon (1987) found that both in Manitoba and at Chilkat Pass females return to their natal areas at lower rates than males, as has been observed in other grouse and most other bird species. Juvenile females that do return never settle on their natal territory (Martin and Hannon 1987). Therefore adult females may not be as pressed as males to defend their territories against juveniles in autumn.

Earlier studies suggested that spring densities of red grouse were regulated by territorial behavior in autumn (Watson and Moss 1972; Watson and Moss 1979). More recently, the importance of autumn territoriality in regulating red grouse populations has been questioned (Hudson 1987). Hannon (1983) suggested that autumn regulation of densities of breeding ptarmigan occurred only in non-migratory ptarmigan populations. However, territorial defence in autumn clearly has some importance, even in migratory ptarmigan.

2.5.2 Movements from breeding grounds

2.5.2.1 Timing and extent of movements

Most ptarmigan stayed in vegetation of, on average, 1m or taller throughout autumn and winter. Hence, ptarmigan may have left their territories because height of vegetation decreased below 1m as snow depth increased. Mossop (1987) also concluded that ptarmigan at Chilkat Pass leave their territories when vegetation above snow level is less than 1m tall. During his study most migration did not occur until February, when snow depth reached 1m in open areas. In both winters of my study, ptarmigan left the breeding grounds in mid-December. There was less snow in open areas in December 1988 than at the same time in 1987, but in 1988 heavy wind redistributed the snow into the shrubs, leaving little in open areas. Furthermore, heavy, wet snow bent most shrubs, which further decreased height of vegetation. The decrease in height of vegetation is ultimately caused by snowfall, as Mossop suggested, but the differences in snow distribution between the two years show that wind plays an important role in determining uncovered height of vegetation. Therefore, departure of ptarmigan from their breeding grounds is ultimately caused by lack of cover and food, which in turn is caused by a combination of snow depth and wind speed. The gradual movements of ptarmigan and changing of wintering grounds during winter, as Mossop (1987) also observed, reflect changes in local conditions over the winter.

Ptarmigan that remained on Datlasaka Flats throughout the winter clearly selected those parts of the flats which were protected from high winds. The high winds on the breeding grounds redistributed much of the snow into the vegetation, leaving little exposed, and cause blowing snow to abrade any exposed vegetation (Formozov 1963). The latter effect partly explains the difference in height of vegetation between the Haines Road habitat site, which was situated directly in line with the Kelsall and the Tatshenshini River valleys (See Appendix 1), and other sites. The West Haines Road snow site is slightly more protected from the high winds because it lies behind a moraine, which deflects some of the wind northward. This resulted in a smaller difference in snow depth between open and vegetated areas at that site than at the Haines Road site. High winds also increase convective heat loss of animals (Marchand 1987). The difference in wind speed between the breeding area and the wintering grounds (Kelsall Lake) was striking, and explains why in both years large numbers of ptarmigan were seen at Kelsall Lake, and not closer to the breeding area, 5km away.

Weather conditions also control winter movements of other grouse species. Colorado white-tailed ptarmigan arrive in their wintering grounds gradually, starting in the third week of October, but later in an autumn with extended mild weather (Hoffman and Braun 1977). They also avoid areas with high winds (Braun and Schmidt 1971), presumably because wind speed affects distribution of plants used by ptarmigan. Alberta white-tailed ptarmigan remained in alpine habitat in a winter with little snow, but left in a winter with much snow (Herzog 1980). During mild winters in Switzerland only half of female and few male rock ptarmigan move downhill towards the boreal forest, whereas in severe winters nearly all birds of both sexes move downhill (Bossert 1980). Snow depth also influences winter movements of sharp-tailed grouse (Tympanuchus phasianellus; Swenson 1985) and sage grouse (Dalke et al. 1963; Beck 1977; Dunn 1984). Clearly, local conditions account for the plasticity in the timing and extent of winter movements by grouse (Herzog 1980). Thus, variation in snow cover between years will influence movement patterns.

2.5.2.2 Timing of return to breeding grounds

In 1989 males returned to their territories 2-3 weeks earlier than females. Similarly, males returned earlier to their territories in populations of rock ptarmigan (Weeden 1964; Gardarsson 1987), blue grouse (Anthony 1903; Bendell and Elliott 1967), and migrating spruce grouse (Herzog and Keppie 1980). There was a strong relationship between the time males returned to their territories and the distance they had to move from their wintering grounds. Moreover, the first males returned to their territories at approximately the same date both years, regardless of snow depth at the breeding grounds. Thus, timing of return by males is probably controlled by an external factor such as photoperiod. In contrast, females may adjust the timing of return to the breeding grounds to weather and snow conditions, as has been documented for other migrants (Lewis and Farner 1973). Especially in females environmental factors other than day length appear to play an important role in gonadal development (Lewis and Farner 1973). This accounts for the poorer correlation between the timing of female return and the distance females moved from the breeding grounds. Moreover, females that wintered nearby did not settle on their territories earlier than those that wintered at a greater distance. Hence, with respect to obtaining a territory there appears to be no advantage to wintering nearby for females (assuming individuals arriving earlier would have a better chance of obtaining a territory). Mortality of females that moved to the boreal forest was not significantly higher than that of females that remained in alpine habitat, but sample sizes were small (Chapter 3). However, there may be other advantages to wintering nearby, such as lower movement-related energy expenditures.

Nearly all ptarmigan left their territories for short periods in both autumn and spring. These departures appeared to be related to periods of bad weather. Pedersen et al. (1983) and Thingstad (1984) observed movements of willow ptarmigan from their territories during bad weather after territorial behavior had started in spring. This has also been observed in rock (Bossert 1980) and white-tailed ptarmigan (Braun et al. 1976). Red grouse leave their territories and form flocks during snow storms in winter (Jenkins et al. 1963). Spring storms delayed gonadal development in male song sparrows (Melospiza melodia) and white-crowned sparrows (Zonotrichia leucophrys), and caused nearly all birds to leave their territories (Wingfield et al. 1983; Wingfield 1985). Clearly, availability of cover and food, and absence of high winds outweighs the benefit of territory occupation. Temporary departures from territory, then, are analogous to movements from the breeding grounds in winter.

Snowfall and high winds can hinder feeding and eliminate shelter rapidly. Moreover, snowfall from one storm could bury most vegetation, and searching for better cover during a storm would be energetically expensive. Therefore, it is advantageous for ptarmigan to be able to predict when storms occur, so they can leave their territories and reach protected locations (see Buttemer 1985). Changes in feeding behavior prior to storms have been observed in other species of birds (Buttemer 1985). Storms are usually preceded by a drop in atmospheric pressure (Battan 1984). As homing pigeons (Columba livia) are sensitive to very small changes in pressure (Kreithen and Keeton 1974), they, as well as other species, may use such changes to predict storms. Although pressure intensity was low when ptarmigan at

Chilkat Pass left their territories, ptarmigan did not leave during all decreases in pressure. Nor were all storms preceded by declining pressure. Therefore, ptarmigan probably use additional cues to predict the arrival of storms.

2.5.3 Segregation of the sexes

During winter 1988-89 most males remained in alpine areas within 20km of their territories, whereas most females moved farther, into the boreal forest. In winter, temperatures in the boreal forest are lower than in alpine habitat near Chilkat Pass (Mossop 1987). Although wind speeds in alpine habitat tend to be higher, males also avoid areas with high winds. Thus, it appears that females were exposed to a colder environment despite the fact that females are approximately 10% smaller than males (S. J. Hannon, pers. comm.). This contradicts the body size hypothesis. Before females moved to the forest, the sexes were partly segregated, as all males, but only half of the females were on their territories. Hence, it is unlikely that male dominance forced females to leave alpine habitat, as suggested by the dominance hypothesis. Aside from wintering closer to the breeding grounds, males left their territories later and returned earlier than females. These findings support the arrival time hypothesis. However, this hypothesis does not explain why segregation was incomplete. To satisfy the hypothesis, all males should remain as close to the breeding grounds as possible to be assured of a territory the following spring. Similarly, if females moved to the forest to take advantage of high quality foods not available near the breeding grounds (Herzog 1980), one would expect all females to move there every winter, regardless of snow depth near the breeding grounds. On the contrary, food habits during winter are similar for both sexes of rock (Bossert 1980) and white-tailed ptarmigan (May and

Braun 1972). Thus, no single factor hypothesis can satisfactorily explain segregational movements of the sexes in willow ptarmigan.

The migration threshold hypothesis, on the other hand, does explain incomplete segregation of the sexes. The migration threshold may not only differ between sexes, but also between individuals of one sex. I found no significant difference in age of short and long distance migrators, but Ketterson and Nolan (1983) suggest that experienced breeders are often able to reclaim their territories, even if they are not the first to arrive on them. Experimentally removed male great tits (_Parus major_) are able to reclaim their territories from replacements, although the chance of doing so decreases when the owner is off its territory for several days (Krebs 1982). There may be additional, undetected intrasexual differences that explain the incomplete segregation of the sexes. As a similar incomplete segregation occurs in juncos (Ketterson and Nolan 1983), these intrasexual variations are probably not specific to ptarmigan, but to differential migrants in general.

Sexual segregation appears to occur in most winters because males have a higher migration threshold than females, and thus remain closer to the breeding grounds than females. However, in winters with little snow, when plenty of cover and food is available on the breeding grounds, both sexes will stay on or near their territories. This is consistent with patterns among red grouse which, in the absence of regular snowfall, are not forced to move from the breeding grounds, except during occasional snow storms (Jenkins _et al_. 1963). Females of that species remain in the vicinity of the breeding grounds throughout the winter (Jenkins _et al_. 1963). Other migratory species have also changed their winter movement patterns when food availability near the breeding grounds changed (Welty 1982).

During winter the sexes segregate spatially through differential migration, but others have observed segregation of grouse within the same area as well. Among white-tailed ptarmigan some segregation of the sexes occurs during autumn (Schmidt 1969). Within wintering areas male and female willow (Mossop 1987) and white-tailed ptarmigan (Braun and Schmidt 1971) often form distinct flocks. The sexes of capercaillie (Tetrao urogallus) and black grouse (T. tetrix) segregate in winter, but occupy different habitat within the same area (Koskimies 1957; Seiskari 1962). In my study, some segregation of males and females appeared to take place during winter molt, but I could not quantify it. Hence, in grouse segregation may not be related to migration alone, but may occur at any time birds are in flocks off their territories. Differential cover requirements could play a role, as sage grouse use the same habitat in winter, but females remain in denser sagebrush than males (Beck 1977). More intensive study of movements and habitat use during periods in which grouse are off their territories but in the same area may provide important cues to the causes of segregation in these species (Weeden 1964).

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CHAPTER 3 NATURAL MORTALITY OF WILLOW PTARMIGAN AT CHILKAT PASS, B.C.

3.1 INTRODUCTION

Predation is thought to play an important role in population dynamics of grouse (e.g. Kenward and Marcström 1986; Bergerud 1987; Lindström et al. 1987; Marcström 1987). Hence it is essential to understand mortality patterns throughout the year. Vulnerability to predation is likely to differ with time of the year because the timing of reproductive effort varies between the sexes: males defend territories in spring, whereas females incubate eggs and raise young in late spring and summer (see Clutton-Brock et al. 1982). Moreover, males and females of most grouse species segregate after the breeding season and spend the winter in different habitats (Hines 1986; Chapter 2). As a result, the sexes may suffer differential mortality.

Numbers of willow ptarmigan (Lagopus lagopus) in North America cycle with a periodicity of 8-11 years (Hannon and Barry 1986; Mossop 1987). During the winter most male ptarmigan are thought to remain in alpine areas close to the breeding grounds, whereas most females probably move to the boreal forest (Weeden 1964; Höhn 1984; Mossop 1987; Chapter 2). Snowshoe hares (Lepus americanus) in the boreal forest also undergo cyclic fluctuations in numbers with the same period as ptarmigan (Krebs et al. 1986). It has been suggested that predators in the boreal forest switch to grouse when populations of hares or voles decline (Hörnfeldt 1978; Angelstam et al. 1984; Keith and Rusch 1986). Hence, females wintering in the boreal forest may suffer higher mortality than males. Hannon and Barry (1986) observed a shortage of female willow ptarmigan in the NWT, which they suggested was caused by higher mortality of females during winter. However, Mossop (1987) observed that willow ptarmigan at Chilkat Pass, B.C. did not move from the breeding area until February. Thus, if females suffer higher mortality during winter, this could occur not only on the wintering grounds, but also on or near the breeding grounds between the end of the breeding season and winter migration. Martin (1985) attributed a shortage of female willow ptarmigan on her study area to lower philopatry of females. Breeding site fidelity at Chilkat Pass, however, is high for both males and females (Schieck and Hannon 1989).

Earlier, Hannon and Gruys (1987) studied remains of depredated willow ptarmigan to examine patterns of predation in this species at Chilkat Pass, but they could not determine the fate of all ptarmigan during winter, as remains were only collected on the breeding area. Other studies that documented disappearance of ptarmigan outside the breeding season used counts, searched for remains, or both (e.g. Jenkins et al. 1964; Braun and Rogers 1971; Gardarsson 1987). These methods produce an estimate of total disappearance, but do not explain its causes. Moreover, results are influenced by search effort. However, with the advent of radio telemetry, it has become possible to follow individual ptarmigan from one breeding season to the next, and document their fates. Accordingly, in the present study I use radiotelemetry to examine when and where mortality of adult male and female willow ptarmigan occurs outside the breeding season at Chilkat Pass. Moreover, I compare mortality during autumn and winter to mortality of birds that were radio-tagged during the breeding season as part of other projects.

The common predators of adult ptarmigan on the subalpine breeding area at the Chilkat Pass are red foxes (Vulpes vulpes), gyrfalcons (Falco rusticolus), and short-tailed weasels (Mustela erminea), which are present throughout the year (Weeden 1960; Mossop 1987; O'Reilly and Hannon 1989), as well as northern harriers

(*Circus cyaneus*; Hik *et al*. 1986) and golden eagles (*Aquila chryseatos*) during the summer (Weeden 1960; Mossop 1987). Bald eagles (*Haliaeetus leucocephalus*), peregrine falcons (*F. peregrinus*), and goshawks (*Accipiter gentilis*) migrate through Chilkat Pass during spring and fall (Weeden 1960). In the nearby boreal forest north of Chilkat Pass goshawks, great horned owls (*Bubo virginianus*), coyotes (*Canis latrans*), and lynx (*Lynx lynx*) are common throughout the year (Boutin *et al*. 1986). Foxes may use forested areas as well (S. Boutin, pers.comm.).

3.2 METHODS

3.2.1 Capture, marking, and radio telemetry

I conducted this study from September 1987 to March 1988 and August 1988 to April 1989 at Chilkat Pass in northwestern British Columbia (59°50'N., 136°35'W.; Appendix 1). Data on mortality during the breeding season were collected from May to July of 1986-1989. The topography, vegetation, and climate of the area are described in Appendix 1. As part of other studies approximately 95% of ptarmigan on a 4.5 km^2 study area were captured and marked with a unique combination of an aluminium and three plastic color bands (Martin and Hannon 1987; Schieck and Hannon 1989). Sexes were distinguished on the basis of differences in plumage and voice (Martin and Hannon 1987), and ages were determined by comparing pigmentation on the eighth and ninth primary (Bergerud *et al*. 1963). The same area was searched for marked birds each spring, and the percentage of returning birds calculated. Some banded birds were killed by hunters each winter (Chapter 4), but I did not take those losses into account, as the number of bands returned by hunters varied with collection effort

(Chapter 4). Moreover, hunting pressure on banded birds was similar in all years (Chapter 4).

In July 1987, nine males and nine females were equipped with 18g radio transmitters (Austec, Edmonton, Alta.), which had a life expectancy of up to five months (Appendix 2). In July of 1988, I equipped 23 territorial males and 26 resident females with transmitters with a battery life of one year (Biotrack, Wareham, Dorset, UK; Appendix 2). During the breeding seasons of 1986-1989 53, 74, 82, and 71 resident females respectively, were equipped with 21g transmitters (Austec) with a battery life of 4-5 months. In 1988 and 1989 17 and 30 territorial males, respectively, were also tagged (21g Austec), and followed from May to July. All collars were attached with a necklace made of harness wire (Schieck 1988; Appendix 2), or soft cord (Kenward 1987). I tracked radio-tagged birds with hand-held Yagi antennas. I tried to locate each bird visually at least once a week, but once ptarmigan left the breeding area this was often not possible because many were inaccessible. During the breeding seasons birds were visually located 2-5 times per week.

To determine whether radiotagging affected survival of individuals, I compared overwinter survival of collared birds with that of individuals with leg bands only. For males, breeding season (See Section 3.2.3 for definition) mortality was negligible (see Section 3.3.4). Hence, survival of leg-banded males was defined as the percentage of males counted in spring that returned in a subsequent spring. For females I used the percentage of females counted after their chicks hatched that returned the following spring. Females that lost their nests were often very secretive, and as a result were easily missed overlooked. Therefore I used only leg-banded and radio-tagged females that successfully hatched chicks in comparing female overwinter survival. I excluded all birds killed by hunters. Schieck and Hannon (1989) found that only 10% of males and 31% of females switched territories between years, and 60% of those that switched occupied the neighboring territory. Thus, emigration was not taken into account.

3.2.2 Predator Identification

During field work all sightings of predators were recorded. Foxes were less likely to be observed when there was no snow on the ground (Hannon and Gruys 1987). Therefore, during the non-breeding season only mammal sightings after October 24 (date of first snow cover (Chapter 2)) were used. During the breeding season only fox sightings between April 22 (first day that data were available for all years) and 2 weeks before average date of clutch initiation were used. Average date of clutch initiation is correlated with date of snow melt (Hannon et al. 1988). Because tracks are easily counted more than once, I excluded them from the analyses.

Whenever possible, dead radio-tagged ptarmigan were collected, and the remains along with any sign of predators, were described. During the periods in which ptarmigan were on or near their territory (April-September), the date of predation was nearly always known within 5 days. However, the mortality date of birds that were depredated during winter in inaccessible areas had to be estimated from the freshness of the kill and depth of snow on the remains (see Hannon and Gruys 1987). I classified predators as either mammals (mostly red foxes), raptors, or unidentified predators (Hannon and Gruys 1987). To determine the identity of the predator, I compared the remains to those killed by known predators, and to descriptions in the literature (Einarsen 1956; Hannon and Gruys 1987). However, it was not always possible to establish cause of death, because in some cases little or no remains could be found. Moreover, ptarmigan may have been depredated after they were weakened by parasitism (Duncan et al. 1978) or food shortage (see McGowan 1969), or wounded by hunters (Mercer 1967). Scavengers could also have concealed the identity of the predator.

3.2.3 Data analysis

Sixteen of 432 radio-tagged birds were killed within 10 days of tagging. Boag (1972) found that radio-tagged red grouse were less active and ate less than non-tagged grouse within one week of tagging, but that the differences diminished after that. To minimize the influence of handling on mortality, I excluded all birds killed within 10 days of tagging from the analyses.

I divided each autumn and winter into six time periods of approximately 60 days each (except winter molt, which was 30 days; Chapter 2). I based the periods on changes in migratory behavior. When I could not determine exactly when a bird changed its behavior (e.g., on what date it moved from its brood rearing area to winter molting area) I used the average date of all tagged birds. The periods were defined as follows, with average dates for all birds in brackets: brood rearing, from Aug. 1 (start of the study) until the onset of winter molt (Sept. 23), winter molt, molt into winter plumage (Sept. 24-Oct. 23), autumn territoriality, from the time ptarmigan returned to their territories in October-November until they left in November-December (Oct. 24-Dec. 10), early winter movements, from the time ptarmigan left the breeding grounds until Jan. 31, late winter movements, from Feb. 1 until ptarmigan returned to their territories in spring, and transient spring territoriality, from the time ptarmigan first returned to their territories in spring until they settled permanently.

The breeding season was defined as the time from permanent settling on their territories to the time chicks fledged. However, because birds were not radio-tagged immediately upon settling on their territories, I only calculated mortality for the following six periods of approximately 10 days each, based on stages of nesting: early pre-laying (20 days before date of first egg (DFE) until 11 days before DFE), late pre-laying (10 days before DFE until DFE-1), laying (DFE until incubation started), early incubation (first 11 days of incubation), late incubation (last 10 days of incubation), and pre-fledge (hatching until 10 days post hatching). DFE and hatch date were determined using the methods described by Hannon et al. (1988). When females lost their nests to predation, their transmitters were removed. Therefore, after egg laying started I used only females that hatched young, or were killed during nesting, in the analyses. In the analysis of female mortality I examined the effect of hatch date on female mortality in fall. The span of hatching dates was divided into three periods. The middle period was defined as mean hatch date (first nests and renests combined) ±0.5 SD. Early and late periods were dates before and after the middle period, respectively (Hannon et al. 1988).

I calculated Kaplan-Meier survival estimates and standard errors (Pollock et al. 1989) for each sex and time period separately. This method allows birds to be removed ("censored") from the sample during the study (Pollock et al. 1989). Hence, hunter-killed or lost birds could be included in the sample. For reasons that I will explain in the discussion I assumed for the analyses that all lost ptarmigan had not emigrated, but were killed. I used a generalized Kruskal-Wallis H-Test (Eq. 5.29, p. 144 in Lee 1980) to determine if survival curves were significantly different among years or between sexes. When a test was not significant in two or more years, but data in each of the years showed a trend in the same direction, I combined the probabilities (Sokal and Rolph 1981). I considered differences significant when P values were less than 0.05.

3.3 RESULTS

3.3.1 Return of leg-banded ptarmigan

Since 1981 the percentage of females counted in the previous spring that returned to the breeding area was not significantly lower than that of males in individual years except 1986 (Table 3-1; S. Hannon, unpubl. data). However, when P-values since 1981 were combined (Sokal and Rolph 1981), the return rates of adult females were significantly lower than those of adult males.

3.3.2 Effect of radio transmitters on predation

Transmitter weight ranged from 2.3-5.2% of body weight in May (ave.=3.0%, SE=0.09%, n=44), but I found no significant correlation between the number of days radio-tagged birds survived from the start of the study and the ratio of transmitter weight to body weight (Spearman rank correlation; r_s=0.16, P>0.05). In both years overwinter survival of radio-tagged ptarmigan was not significantly different from return rates to territory of leg-banded birds (Table 3-2).

3.3.3 Mortality outside the breeding season

During both years of the study the levels of male and female mortality during the non-breeding season were not significantly different (Figure 3-1; 1987-88: χ^2=1.05, df=1, P=0.29; 1988-89: χ^2=1.10, df=1, P=0.27; combined: $-2\Sigma \ln P$=5.05, df=4, P>0.1). Mortality of females and males outside the breeding season in 1987-88 was not significantly different from 1988-89 (Females: χ^2=0.66, df=1, P=0.51; Males: χ^2=0.63, df=1, P=0.53). However, sample sizes in 1987-88 were low. Within all time periods of

Table 3-1 **Percentage of marked adult willow ptarmigan at Chilkat Pass observed in one spring returning to the breeding grounds the next spring at Chilkat Pass, B.C. (S. Hannon, unpubl. data)**

Year Returning	Males			Females				
	Ret.	95% C.I.	n	Ret.	95% C.I.	n	G[1]	P Value
1980[2]	41.0	0.24-0.59	29	53.7	0.40-0.67	54	1.13	0.29
1981	48.1	0.29-0.67	27	42.5	0.31-0.54	73	0.25	0.62
1982	41.5	0.26-0.57	41	30.4	0.12-0.49	23	0.75	0.39
1985	50.0	0.34-0.66	36	42.0	0.28-0.56	50	0.53	0.47
1986	61.0	0.52-0.70	118	38.9	0.30-0.48	113	11.28	<0.001
1987	57.9	0.49-0.67	121	52.2	0.44-0.61	134	0.81	0.37
1988	63.4	0.53-0.74	82	50.9	0.41-0.61	102	2.85	0.09
1989	57.3	0.46-0.69	75	42.7	0.32-0.53	82	3.34	0.07
Combined Probabilities 1981-1989							30.87[3]	<0.01

[1] Results from G-Test to test difference in return rates between males and females.

[2] Return from spring 1979 to spring 1980.

[3] $-2\Sigma(\ln P)$ for 1981-1989; P value result of χ^2 Test (Sokal and Rohlf, 1981).

Table 3-2 Overwinter survival of radio-tagged and leg-banded willow ptarmigan at Chilkat Pass, B.C. during 1987-88 and 1988-89

	Females[1]			Males		
	Surv.	95% C.I.	n	Surv.	95% C.I.	n
1987-88						
Radio-tagged	0.50	0.10-0.90	6	0.65	0.34-0.96	9
leg-banded	0.67	0.47-0.87	21	0.59	0.49-0.69	95
G[2] (P)	0.49 (0.48)			0.20 (0.66)		
1988-89						
Radio-tagged	0.32	0.11-0.53	19	0.43	0.24-0.62	22
Leg-banded	0.44	0.27-0.61	32	0.48	0.34-0.62	48
G (P)	0.73 (0.39)			0.29 (0.59)		

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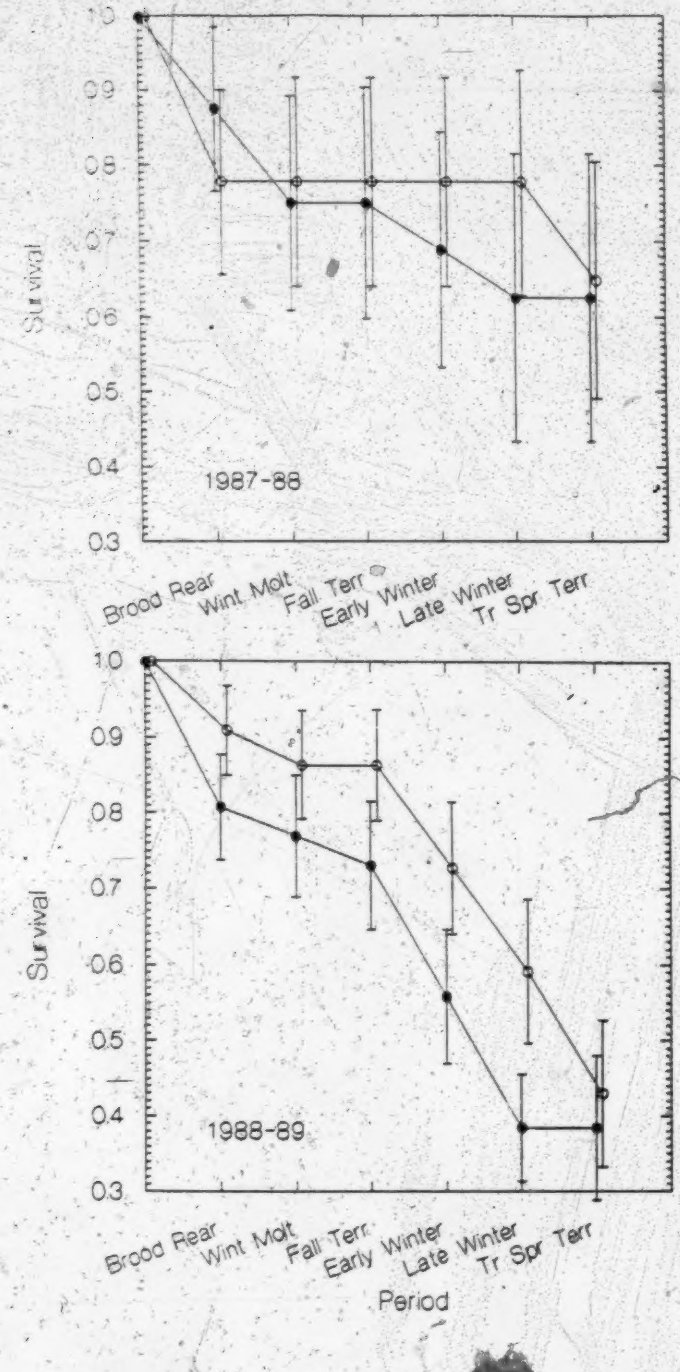
[1] Females with successful nests only.

[2] Results of G-Test, comparing survival of leg-banded and radio-tagged birds.

Figure 3-1 a. Kaplan-Meier survival estimates ±SE of radio-tagged adult male (O; n=9) and female (●; n=8) willow ptarmigan during fall and winter of 1987-88.

b. Kaplan-Meier survival estimates ±SE of radio-tagged adult male (O; n=22) and female (●; n=26) willow ptarmigan during fall and winter of 1988-89.


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
Survival
1987-88
Brood Rear
Wint. Molt
Fall Terr
Early Winter
Late Winter
Tr Spr Terr
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
Survival
1988-89
Brood Rear
Wint. Molt
Fall Terr
Early Winter
Late Winter
Tr Spr Terr
Period

both 1987-88 and 1988-89 mortality of males and females was similar (data from Figure 3-1; G-RAN Test; $P>0.1$ for all periods).

In both years nearly all autumn mortality occurred during brood rearing and winter molt (Figure 3-1). In 1987 survival from hatch to 15 September of females with broods was 0.75 (3 of 4, SE=0.217), and in 1988 0.74 (14 of 19, SE=0.101), whereas no females (1987: 0 of 4; 1988: 0 of 5) without broods were killed in either year. Thus, travelling with broods may put females at greater risk. However, survival of females with chicks was not significantly less than of those without chicks, although sample sizes were small (1987: $\chi^2=0.75$, df=1, $P=0.45$; 1988: $\chi^2=1.20$, df=1, $P=0.23$; combined: $-2\Sigma(\ln P)=4.53$, df=4, $P>0.1$). Survival of females with chicks that hatched late was similar to that of females that hatched chicks in the middle period (late: surv.=0.80, SE=0.13, n=10; middle: surv.=0.86, SE=0.13, n=7). Survival of females with early hatched chicks appeared low (surv.=0.50, SE=0.35, n=2), but sample size for that period was too small to be meaningful.

Male willow ptarmigan remain with their mate and chicks during brood rearing (Wittenberger 1978), and thereby could help protect their mate from predation. Hence, one would expect survival of a female with chicks to be greater if she is accompanied by her mate. However, mortality of females that were unaccompanied by their mate during the brood rearing period of 1988 was not significantly different from mortality of females accompanied by their mate (accompanied: surv.=0.71; SE=0.14, n=7; not accompanied: surv=0.63, SE=0.17, n=8; $\chi^2=0.52$, df=1, $P=0.77$). I could not compare these two groups of females for 1987, as I did not start tracking birds until September of that year.

Males that accompanied their mate and brood could be expected to suffer predation similar to females during the brood rearing period. However, both males killed in August or early September of 1987 had mates without broods. In 1988 one of the two males killed had probably left its mate. The other one was seen with its mate and brood until it was killed. However, males that accompanied females in fall often remained at 10-50 m. from the brood, and were less conspicuous than the female and chicks. This may have reduced their risk of predation.

Part of the ptarmigan population left their territories during August and moved uphill (Chapter 2). In 1988 ptarmigan that left their territories had survival rates similar to those that stayed in the vicinity of their territories (females: stayed: surv.=0.80, SE=0.11, n=10; left: surv.=0.75, SE=0.13, n=12; unknown if left: surv.=1.00, n=4; χ^2=0.87, df=1, P=0.65; males: stayed: surv.=0.92, SE=0.08; left: surv.=0.89, SE=0.11, n=9, unknown if left: surv.=1.00, n=1; χ^2=0.18, df=1, P=0.91; no data for 1987).

The second peak in mortality occurred when ptarmigan were on their wintering grounds (Figure 3-1). Although mortality of females that moved into the boreal forest appeared higher than that of females remaining in alpine areas (forest: surv.=0.40, SE=0.16, n=10; alpine: surv.=0.80, SE=0.18, n=5), the difference in survival was not significant (χ^2=1.14, df=1, P=0.17). Mortality of males that moved past the edge of the forest was similar to the mortality of those that remained near the breeding grounds (forest: surv.=0.75, SE=0.22, n=4; alpine: surv.=0.69, SE=0.18, n=16; χ^2=0.35, df=1, P=0.73). When sexes were combined, mortality of birds that moved to the boreal forest was not significantly different from mortality of birds remaining in alpine habitat (forest: surv.=0.50, SE=0.11, n=14; alpine: surv.=0.71, SE=0.13; n=21; χ^2=0.70, P=0.48).

Male mortality was as high during spring transient territoriality as during early and late winter movements, whereas no females were killed during the spring transient territoriality period (Figure 3-1). All males killed during transient territoriality were off their territories.

3.3.4 Mortality during the breeding season

During every breeding season females suffered most mortality during late prelaying, late incubation, and pre-fledging (Figure 3-2). Mortality of females during the breeding season varied significantly among years (data from Figure 3-2; $\chi^2=24.0$, df=3, $P<0.001$), from 5% to nearly 30%.

In both years that males were radio-tagged during the breeding season, they all survived (1988: n=17; 1989: n=27). The survival curves of males and females were not significantly different in 1988, but males suffered significantly lower mortality in 1989 (1988: $\chi^2=1.27$, df=1, P=0.21; 1989: $\chi^2= 3.46$, df=1, P=0.002).

3.3.5 Lost birds

During the study I lost no radio-tagged males, but in 1987-88 one of the females that was radio-tagged during autumn disappeared in December. In 1988-89 I lost four radio-tagged females during the winter. Two were last seen in November on the breeding grounds, while two others were last heard in the Tatshenshini River valley, north of the breeding grounds (Appendix 1). One of the latter two was lost in February, and the other one in late March. These lost females may have been depredated outside the area I searched (see Chapter 2), or their transmitters could have failed after which they were depredated. This is quite plausible, since in spring 1989 two females and one male returned to the breeding grounds with failed transmitters.

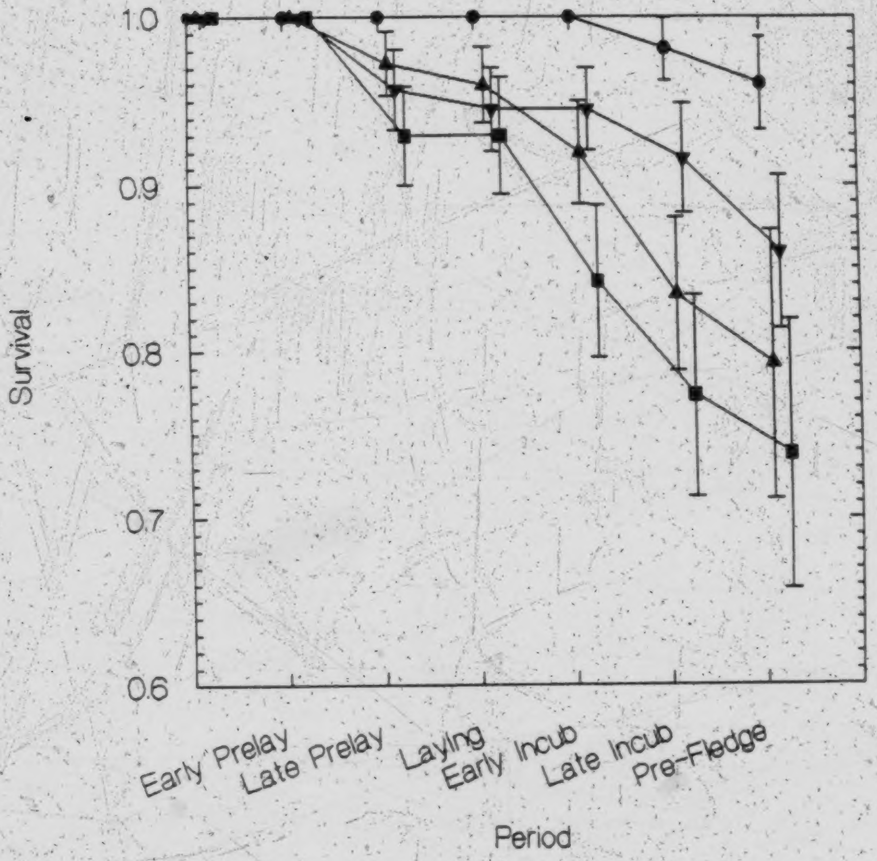


Figure 3-2 Kaplan-Meier survival estimates ±SE of radio-tagged adult female willow ptarmigan during the breeding seasons of 1986 (●; n=47), 1987 (▴; n=35), 1988 (▾; n=55) and 1989 (■; n=37).

3.3.6 Predator identity and sightings

Both males and females were most often killed by raptors during autumn and spring. Predation during these periods coincided approximately with the onset of autumn and spring raptor migration (Figures 3-3 and 3-4). Females killed in winter for which I could establish cause of death were also taken by raptors. These were all females which were killed in the boreal forest. There appeared to be no difference in predator identity between males and females, although some males were killed by mammals (mostly foxes), whereas females were not (Table 3-3).

Resident gyrfalcons were observed sporadically in subalpine areas throughout the winter. Tracks of foxes, wolves, weasels, and wolverines were observed in subalpine habitat throughout each winter, but mammals were sighted only sporadically (Table 3-4). In the boreal forest goshawks and great horned owls were observed throughout each winter, as were coyotes and one lynx, but too little time was spent in the forest to quantify their numbers. In spring 1988 the number of raptor sightings did not increase as it did in spring 1989 (Table 3-4), but in 1988 fieldwork was halted before the onset of spring raptor migration.

During the breeding seasons of 1986 and 1987 all identified kills were made by raptors, in 1988 ptarmigan were taken by both raptors and foxes, but in 1989 foxes were the major predators (Table 3-5). However, in 1989 only few of the depredated ptarmigan were collected for predator identification. Mammals and raptors killed female ptarmigan at similar levels during each stage of the breeding season (Table 3-5). The level of mammalian predation was not significantly correlated with the number of fox sightings on the breeding grounds, but nearly so (Table 3-6). Years with high raptor predation were not correlated with years with many raptor sightings on the study area (Table 3-6).

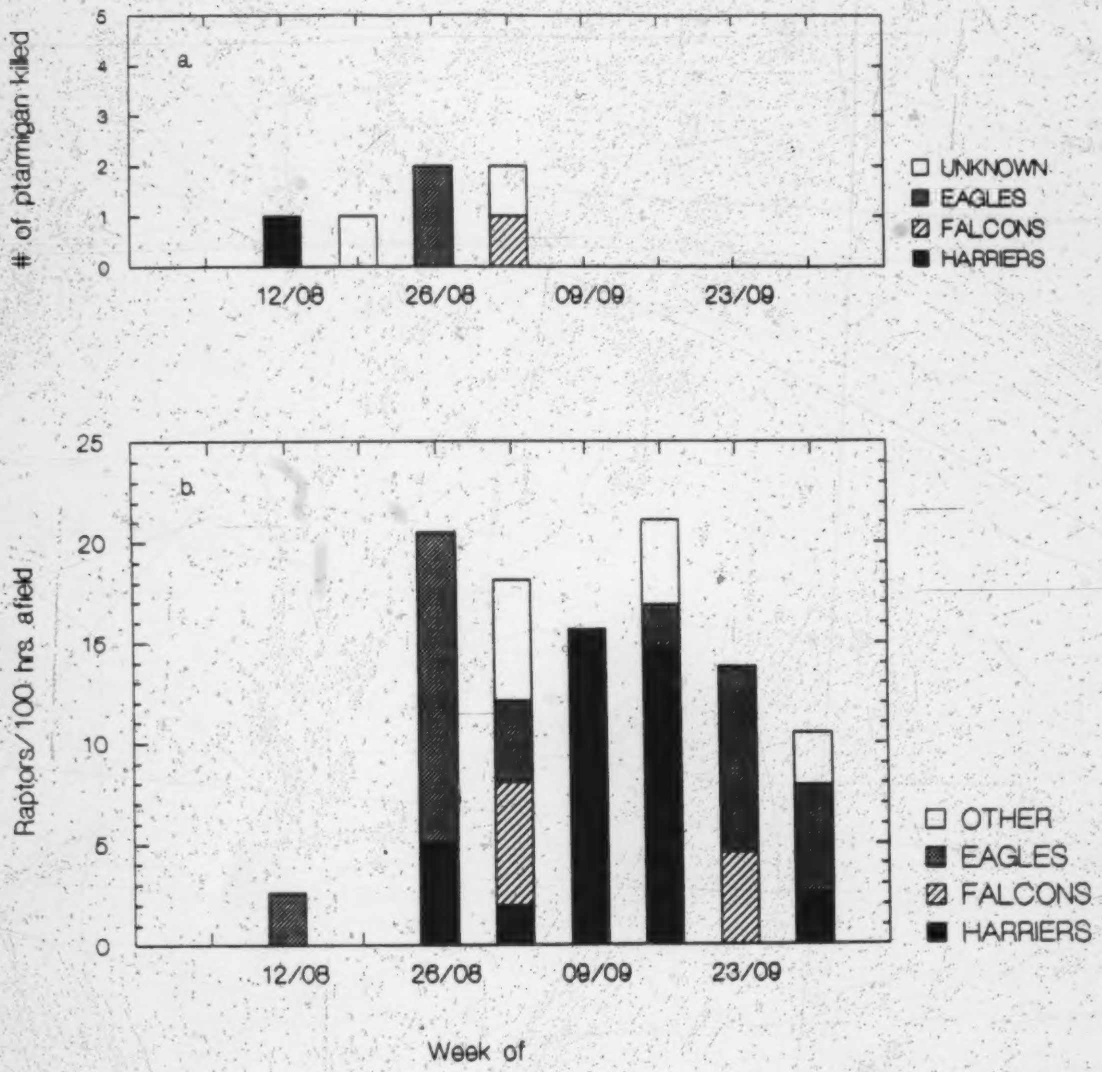


Figure 3-3 a. Number of ptarmigan found killed by raptors in autumn 1988.

b. Number of raptors sighted per 100 hours in the field, autumn 1988. Week of 19/08 was not sampled.

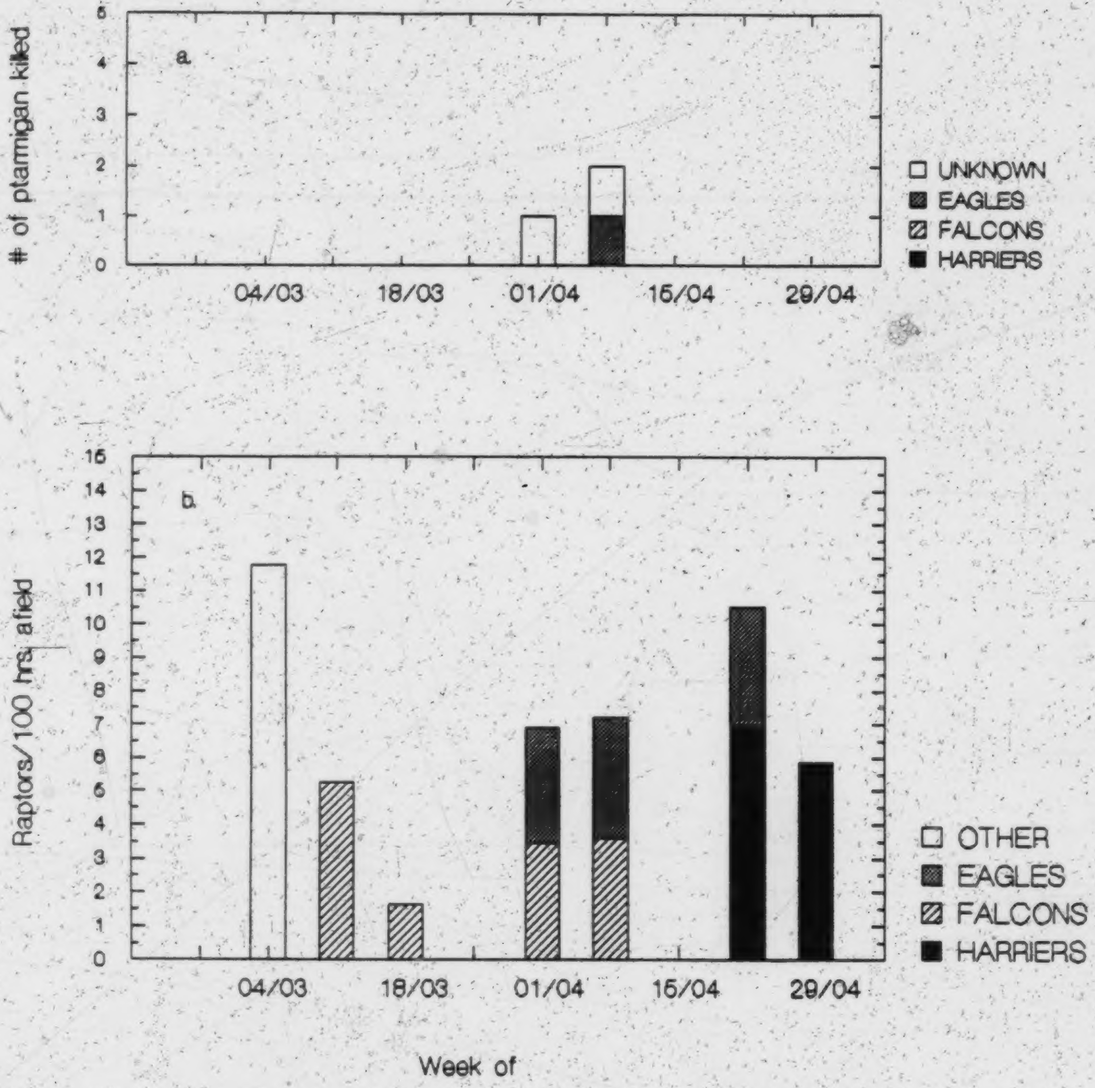


Figure 3-4 a. Number of ptarmigan found killed by raptors in spring 1989.

b. Number of raptors sighted per 100 hours in the field, spring 1989.

Table 3-3 **Cause of death of radio-tagged willow ptarmigan outside the breeding season. Data for 1987-88 and 1988-89 combined.**

Period	Mammal	Raptor	Unident. Pred.	Unknown[1]	Total
Females (n=19)					
Brood Rear	0	6	1	0	7
Winter Molt	0	0	1	0	1
Fall Terr.	0	0	1	0	1
Early Winter	0	1	0	2	3
Late Winter	0	2	2	3	7
Tr Spr Terr.	0	0	0	0	0
Total	0	9	5	5	
Males (n=15)					
Brood Rear	1	3	0	0	4
Winter Molt	0	1	0	0	1
Fall Terr.	0	0	0	0	0
Early Winter	0	0	2	1	3
Late Winter	1	0	1	1	3
Tr Spr Terr.	1	2	1	0	4
Total	3	6	4	2	

[1] Fate unknown, bird never found.

Table 3-4 **Number of predator sightings per 100 hours in the field during the non-breeding season in subalpine habitat at Chilkat Pass, B.C.**

Period	Hours	Foxes	Other Mammals[1]	Harriers	Falcons[2]	Eagles[3]	Other Rapt.[4]	Total Rapt.
1987-88								
Brood Rear	40.3	-	-	12.4	5.0	14.9	0.0	32.3
Winter Molt	95.1	-	-	6.3	2.1	6.3	0.0	14.7
Fall Terr	104.9	0.0	1.9	0.0	0.0	3.8	1.0	3.8
Early Winter	77.3	0.0	1.3	0.0	0.0	0.0	1.3	1.3
Late Winter	116.8	1.7	0.0	0.0	1.7	0.0	0.0	1.7
Tr Spr Terr	31.3	0.0	0.0	0.0	0.0	6.4	0.0	6.4
1988-89								
Brood Rear	216.9	-	-	5.1	1.8	4.2	2.3	13.4
Winter Molt	139.8	-	-	2.9	0.0	16.5	3.6	23.0
Fall Terr	155.9	1.9	1.9	0.0	0.6	0.6	0.6	1.8
Early Winter	106.0	1.9	0.0	0.0	0.9	0.0	1.9	2.8
Late Winter	104.7	1.0	0.0	0.0	2.9	0.0	0.0	2.9
Tr Spr Terr	221.3	2.3	0.0	1.8	1.4	1.4	0.0	4.6

[1] Coyotes, wolf, weasel, and wolverine, and unidentified mammals.
[2] Gyrfalcons and peregrine falcons.
[3] Golden and bald eagles.
[4] Goshawks, great horned owls, and unidentified raptors.

Table 3-5 **Identity of predators which preyed on radio-tagged female willow ptarmigan during the breeding season.**

	Mammal[1]	Raptor	Unident.	Total[2]
By year				
1986	0	1	1	2
1987	0	7	5	12
1988	3	5	1	9
1989	5	0	9	14
By period				
Early Prelay.	0	0	0	0
Late Prelay.	2	4	4	10
Laying	1	0	1	2
Early Incub.	2	2	4	8
Late Incub.	2	4	5	11
Pre Fledge	1	3	2	6

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[1] Mostly red foxes.

[2] During the breeding season I classified all deaths as predations, as I found no evidence for other causes of death.

Table 3-6 Number of predators sighted at Chilkat Pass, B.C. per 100 hours in the field during the breeding season[1]

Year	Foxes	Hours[2]	Total Raptors	Harriers	Falcons[3]	Eagles[4]	Other Rapts[5]	Hours[6]
1986	2.4	545.4	9.7	2.3	0.1	3.1	3.2	2443.4
1987	1.0	616.3	6.0	2.3	0.0	2.6	1.1	1715.3
1988	4.7	363.5	7.7	2.0	0.5	2.4	0.2	1351.2
1989	6.1	197.3	5.4	3.3	0.0	1.4	0.3	707.7
r_s[7]	0.95		0.20	-0.26	0.11	0.40	0.0	

[1] Data from S. Hannon (unpubl. data).

[2] Hours between April 22 and 2 weeks before mean date of clutch initiation, used for calculation of fox numbers only. See text.

[3] Gyrfalcons and peregrine falcons.

[4] Golden and bald eagles.

[5] Goshawks, short eared owls, and unidentified raptors.

[6] Hours between April 22 and July 31, used for calculations of raptor numbers only, see text.

[7] Spearman rank correlation coefficient for correlation between mammalian kills and fox sightings, and raptor kills and raptor sightings. $P_{[0.05,4]}=1.00$.

3.4 DISCUSSION

3.4.1 The effect of radio transmitters on risk of predation

Heavier transmitters did not appear to affect survival, but average transmitter weight was below the maximum 5% of body weight recommended by Cochran (1980). During both years of the study, mortality of radio-tagged and banded ptarmigan was similar, but sample sizes were small. Schieck (1988) discussed the effect of breast-mounted radio transmitters on survival and reproductive success of female willow ptarmigan at Chilkat Pass. He reported that females with transmitters had similar survival to the following breeding season, similar reproductive success, and produced chicks of similar quality to those of females without transmitters. However, his sample size for females without transmitters was small, and birds without transmitters were not sighted as often. Erikstad (1979) found no difference in the number of successful nests, clutch size, or chick growth between female willow ptarmigan fitted with breast-mounted transmitters and untagged females. He did observe higher mortality among chicks from females with transmitters, but that could have been the result of brightly colored radio packages. Hines and Zwickel (1985) reviewed the effects of radio transmitters on several species of Tetraoninae. They concluded that transmitters generally had no long-term negative effects on birds, but most studies they reviewed used backpacks rather than necklace designs. Small and Rusch (1985) reported that ponchos were accepted by a higher proportion of ruffed grouse (Bonasa umbellus) than were backpacks, and that there was a trend towards birds with backpacks having lower survival. Hence it may be invalid to estimate the effects of necklace-transmitters from studies using backpacks. Results from this and Schieck's (1986) study suggest that necklace transmitters have no negative long-term effects on willow ptarmigan at Chilkat Pass, but further study is required.

3.4.2 Mortality outside the breeding season

In this study I could not determine if any adult females left their breeding areas and moved elsewhere the following spring. However, female ptarmigan at Chilkat Pass exhibit high breeding site fidelity (Schieck and Hannon 1989), and all females that I lost during winter had bred previously in the same area for one or more years. Hoffman and Braun (1977) and Berry and Eng (1985) found that female white-tailed ptarmigan (L. leucurus) and sage grouse (Centrocercus urophasianus), respectively, also return to the same breeding area each year. Thus, although I cannot rule out emigration by adult females, I believe that it is reasonable to assume that the radio-tagged females that did not return in spring did not emigrate, but were killed during winter.

During both years mortality of males and females outside the breeding season was similar, as was mortality within each period. However, differences may have been masked by small sample sizes. To obtain small variance, Pollock et al. (1989) recommend maintaining 40-50 tagged animals of each sex at any time. However, at Chilkat Pass ptarmigan could only be captured in spring and summer. Thus, with a 60% annual mortality, at least 100 ptarmigan of each sex would have to be tagged to maintain small variances throughout the year.

3.4.2.1 Autumn mortality

High mortality in early September coincided with the onset of autumn raptor migration. However, as migration continued after the period in which most ptarmigan were killed, ptarmigan mortality may be related to other factors as well. Young gyrfalcons gain their independence in the same period (Cade 1960; Dementiew 1960; Poole and Boag 1988). Cade (1960) stated that young gyrfalcons learn their hunting tactics on young ptarmigan. This may also be the case for other raptors. Gardarsson (1987) observed that predation on adult rock ptarmigan was low until four weeks after hatch, when juveniles became more conspicuous. In this study, survival of females with broods was not lower than for females without broods, but sample sizes were small. Herzog (1979) found that spruce grouse (Dendrapagus canadensis) females with broods were three times as vulnerable as those without broods, but he did not report the age of chicks. Nielsen (1986) also observed an increase in predation by gyrfalcons on rock ptarmigan once females had broods. In those periods gyrfalcons switched nearly completely from waterfowl and alcids to ptarmigan. Mortality of female blue grouse (Dendrapagus obscurus) with chicks and adult males in late summer was higher than for unsuccessful females and juvenile males, since the former group remained in open areas, whereas the latter moved to dense forest (Sopuck 1979). Hence, timing of autumn mortality is most likely related to three factors: raptor migration, independence of young predators, and conspicuousness of young ptarmigan.

Bergerud (1970) observed that young that hatched in late summer were more vulnerable to hunting than early-hatched chicks, as they were more conspicuous. I did not collect data on chicks, but younger chicks could attract predators and hence increase vulnerability of the female However, females with younger chicks (i.e. from late first nests or renests) appeared no more vulnerable than those with older ones.

There appeared to be no difference in mortality between individuals remaining on or near their territory and those that moved uphill. Similar uphill movements have been observed in rock ptarmigan (L. mutus) (Gardarsson and Moss 1970; Bossert 1980) and white-tailed ptarmigan, which search for snow accumulation areas in autumn (Braun 1971; Gardarsson 1987), possibly partly to reduce predation risk (Braun 1971). In my study it appeared that only individuals from areas with less cover left their territories during brood rearing (Chapter 2). Thus, these movements may also reduce their risk to predation.

3.4.2.2 Winter mortality

Mortality of ptarmigan that moved to the boreal forest was not significantly higher than that of birds in alpine habitat, but sample sizes were too small to draw definite conclusions. Moreover, during the study the numbers of snowshoe hares in the boreal forest were increasing (Appendix 4), and thus predators may have concentrated on the more numerous hares. Once the hare population declines, predators may switch to ptarmigan wintering in the boreal forest (Keith and Rusch 1986; see Hörnfeldt 1978; Angelstam et al. 1984). I predict that winter mortality of females will increase when numbers of hares decline. The extent of ptarmigan movements in winter is dependent on the amount of snowfall: in years of little snow probably few ptarmigan move to the forest, whereas in years of high snowfall ptarmigan move as far as 100km (Chapter 2). Hence winter mortality of ptarmigan during the decline phase of the snowshoe hare cycle may also be related to snow depth at the breeding grounds.

3.4.2.3 Spring mortality

Unlike females, several males were killed during transient spring territoriality. Males returned to their territories at approximately the same time each spring regardless of snow cover (Chapter 2), but during periods of bad weather they moved off their territories to more protected locations nearby (Chapter 2). All males were killed in the latter areas, or in transit. Unfamiliarity with these protected areas may have resulted in higher predation risk to males. Other populations of ptarmigan also move from their territories in spring during periods of bad weather and form flocks (Bossert 1980; Braun et al. 1976; Pedersen et al. 1983; Thingstad 1984), as do song sparrows (Melospiza melodia) (Wingfield 1985), but there are no records of higher mortality during bad weather in those populations. The extent of movements by ptarmigan to protected areas in spring is related to the frequency of spring storms, and the amount of cover available on the breeding grounds in early spring, which in turn is related to snowfall. Hence, these factors probably influence male mortality in spring.

Male spring mortality coincided with spring raptor migration. The Chilkat Pass is one of only three passes which connect the Yukon Territory to the Pacific Ocean. Hence it acts as a funnel for migrating raptors. This may result in higher predation rates at Chilkat Pass during autumn and spring raptor migration than in areas with fewer migrating raptors.

In spring most females remained in their wintering areas longer than males, and those that returned to the breeding grounds early stayed in small flocks in protected areas (Chapter 2). Most females did not settle on their territories until two weeks after males, when cover was much greater on the breeding grounds (Chapter 2). Moreover, females do not act as conspicuously as males, and they molt into cryptic plumage rapidly (Hannon and Wingfield 1990). Thus, in spring females may have been less susceptible to predation than males.

3.4.2.4 Predator identity

In autumn and winter females appeared to be taken solely by raptors, whereas males were taken by mammals as well. Many remains, however, could not be identified to predator. Hannon and Gruys (1987) found that outside the breeding season most male ptarmigan on the breeding grounds were killed by foxes, whereas females were killed by raptors. This difference was most likely due to the amount of time each sex spent on the breeding grounds. Females were on the breeding grounds mainly during brood rearing and briefly during fall territoriality, and most were killed when raptors migrated through the area. On the other hand, males spent more time on their territories, and therefore had a greater chance of being killed during winter when foxes probably depredated most ptarmigan. Mossop (1987) observed both foxes and gyrfalcons at Chilkat Pass throughout winter and suggested gyrfalcons may take most ptarmigan. He noted an increase in eagle sightings starting in April and presumed they took many ptarmigan, but he presented no quantitative data. As I saw more foxes than gyrfalcons in alpine areas during winter, foxes were probably the main predator of male ptarmigan during winter. In contrast, females which moved past the edge of the boreal forest were exposed to forest-dwelling raptors such as goshawks and great-horned owls, as well as lynx and coyotes. It is not known how many ptarmigan lynx or coyotes take, but D. Murray (pers. comm.) observed attempts by lynx to kill ptarmigan in forested areas. Foxes also range into forested areas (S. Boutin pers.comm.) and probably take ptarmigan there as well.

3.4.3 Mortality during the breeding season

No radio-tagged males were killed after they had settled on their territories in April. Moreover, disappearance rates of banded territorial males was low (S. Hannon pers. comm.). Males spend more time alert while on their territories than females (Williams et al. 1980), which may well decrease their vulnerability to predation. Hence, even if males act as guards for females during the pre-laying period, as argued by Bergerud and Gratson (1987), they do not appear to be vulnerable to predation at that time. Once incubation started, males had molted into their cryptic summer plumage, and territorial behavior declined (Hannon and Wingfield 1990), rendering them inconspicuous. In spring male black grouse (Tetrao tetrix) are killed in habitat where they feed during the day, but rarely on their leks (Angelstam 1984). On the other hand, in their analysis of remains found on the breeding grounds, Hannon and Gruys (1987) found that in spring more males than females were killed. However, most of those males may have been killed while they were off their territory in early spring. In rock ptarmigan, spring predation of males is similar to (Poole and Boag 1988) or greater than of females (Cade 1960; Nielsen 1986). Unlike that among willow ptarmigan, this predation appeared to occur after males had established their territories. The difference between the two species may be related to availability of cover on the territories in spring.

All radio-tagged ptarmigan killed in the breeding season were females. Most predation occurred during late prelaying, incubation, and before chicks fledged. Watson (1956) also noted that more female than male rock ptarmigan and red grouse were killed during the breeding season. Similarly, Martin (1985) and Braun and Rogers (1971) observed that during the breeding season most depredated willow and white-tailed ptarmigan, respectively, were females, but they did not calculate percentage mortality. Unlike willow ptarmigan, female black grouse suffer most predation during laying and early incubation, whereas mortality is low during the pre-laying period and after chicks hatch (Angelstam 1984). Thus, female grouse are vulnerable to predation during the breeding season, but the period of highest vulnerability may vary between species. Differences in timing of predation may also be due to predators involved, although I observed no such differences between raptors and foxes.

As mortality of males and females was similar during both winters, differential yearly mortality did not occur during winter as predicted. On the contrary, females were depredated at a higher rate during the breeding season. Angelstam (1984) found that female black grouse suffered higher mortality during egg laying and early incubation, but not at any other time of the year.. Differential mortality among mallards (Anas platyrynchus) can be largely attributed to red fox predation of females during the breeding season (Johnson and Sargeant, in Angelstam 1984). Increased mortality of females during the breeding season also accounts for differential mortality in great tits (Parus major) (Bulmer and Perrins 1973).

At Chilkat Pass, nesting females suffered between 5 and 26% predation. The variation in predation rate was not caused by changes in the number of observed raptors. Likewise, Redpath (1987) failed to find a relationship between raptor numbers and number of red grouse kills. Yet, Hannon and Gruys (1987) found that over a period of ten years nesting females were killed more often by raptors than by foxes. However, the level of predation by raptors and mammals varied among years. When foxes were numerous, they took more ptarmigan than did raptors, causing high summer mortality. This corresponds with findings from the Islands of Tranøy (Myrberget 1987) and Brunette (Mercer 1967), where ptarmigan suffered less than 5% mortality during the breeding season in the absence of red foxes. Female rock ptarmigan on islands off the coast of Iceland suffered little mortality during the breeding season, in the absence of arctic foxes (Alopex lagopus) (Gardarsson 1987). On the

Icelandic mainland foxes were present, and killed nesting hens (Gardarsson 1987). Hence, the variation in breeding season mortality at Chilkat Pass was probably due to changes in red fox predation. Similarly, Martin et al. (1989) contributed changes in nest failures at Chilkat Pass to changes in numbers of nest predators or availability of alternative prey.

The number of ptarmigan killed by foxes may be related to numbers of small mammals: Voronin (1978) observed high predation of willow ptarmigan during the breeding season in years when lemmings were scarce. Similarly, Marcström et al (1988) observed a positive correlation between vole numbers and fall populations of grouse. In the absence of predators there was no such correlation. They concluded that large vole populations resulted in reduced predation on nesting grouse by generalist predators. Thus, variation in ptarmigan mortality is not caused by predators specializing on ptarmigan, but by predators that switch prey (Voronin 1978). Jones and Theberge (1983) found that the diet of foxes at Chilkat Pass consisted mainly of small mammals during the summer, but they did find foxes to be plastic and opportunistic in their prey selection. Foxes in SW Yukon depended heavily on snowshoe hares when they were numerous, but switched to alternative prey when hare numbers crashed (Theberge and Wedeles 1989). Hence, at Chilkat Pass ptarmigan predation can be expected to be low when small mammals are numerous, as in 1986 (S. Hannon, pers. comm.), and high when few small mammals are available. I have no quantitative data on small mammal numbers at Chilkat Pass, but their numbers probably fluctuate, as occurs in SW Yukon (Krebs and Wingate 1985). There, small mammals were previously thought to fluctuate in a 3-4 year (Krebs and Wingate 1985) or 11-year cycle (Gilbert et al. 1986), but more recent data suggest that their fluctuations are less regular (R. Boonstra, pers.comm.). These oscillations would result in irregular, but fluctuating levels of differential predation on breeding female ptarmigan.

In my study differential mortality took place during summer. However, once snowshoe hare numbers crash, mortality of female ptarmigan wintering in the boreal forest is likely to increase as opportunistic predators switch prey. Clearly, more year-round telemetry studies are required during all phases of the snowshoe hare cycle to examine the role of predation in regulating ptarmigan numbers at Chilkat Pass. Such studies must also take the effect of small mammal fluctuations and weather patterns on ptarmigan numbers into account.

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CHAPTER 4 HUNTING MORTALITY OF WILLOW PTARMIGAN AT CHILKAT PASS, B.C.

4.1 INTRODUCTION

In many species of grouse, one sex predominates in hunter harvests (e.g., Bergerud 1970a; Weeden 1972; Zwickel 1982; Bergerud 1987, and references therein; Moss 1987). It has been argued that those skewed sex ratios were caused by differential natural mortality of the sexes during the breeding season, or differential viability of young (Bergerud 1970a; Bergerud 1987). On the other hand, in blue grouse (Dendrapagus obscurus), skewed sex ratios in hunters' bags were caused by differential movements of the sexes (Mussehl and Leik 1963; Zwickel 1982). Hunting statistics have been used to estimate population composition of willow ptarmigan (Lagopus lagopus) (e.g., Bergerud 1970a; Bergerud 1987). However, during winter male and female ptarmigan segregate: males remain in subalpine areas close to the breeding grounds, whereas females move to the boreal forest (Weeden 1964; Irving et al. 1967; Höhn 1984; Chapter 2). As a result, individuals of one sex may be more vulnerable to hunting, depending on the habitat frequented by hunters. However, the timing of ptarmigan winter movements changes annually (Mossop 1987; Chapter 2). Thus, differential availability of the sexes to hunting may vary among years.

B. C. Fish and Wildlife officials estimated that, in the late 1970s, up to 1000 ptarmigan were killed each winter at Chilkat Pass in northwestern British Columbia (H. Butler, pers. comm.), and hunting continues to the present. Most hunting at Chilkat Pass takes place in subalpine habitat. Hence, males may be more vulnerable to hunting. It is not known, however, if hunters selectively kill male willow ptarmigan. Nor is it known if hunting contributes significantly to overwinter mortality of willow ptarmigan at Chilkat Pass. The hunting season at Chilkat Pass is 6.5 months, whereas in many other areas and species it ranges from several weeks to 4.5 months (e.g., Weeden 1963; Bergerud 1970b; Braun and Rogers 1971; Davies and Stoll 1973; Moss and Watson 1980). Because of this extended season, hunting may have a greater impact on ptarmigan at Chilkat Pass than in areas or species with a shorter season.

In this study I first determined if hunting statistics gave an accurate estimate of population composition. I examined the sex and age composition of hunter-killed ptarmigan from the 1987-88 to the 1989-90 hunting seasons, and compared it to sex composition of radio-tagged individuals (Chapter 2). Second, on the basis of band returns, I assessed what percentage of banded birds available at Chilkat Pass were killed by hunters each year.

The hunting season on ptarmigan in the Chilkat Pass area was open from 15 August-28 February every year, with a daily limit of 10 birds, and a possession limit of 30. The Chilkat Pass is bisected by the Haines Highway which provides year-round access to the area. Virtually all hunting occurs in alpine habitat within 2-3 km. from the road. During the fall and early winter hunters find birds on foot, while after December most of them use snowmobiles.

4.2 METHODS

4.2.1 Study area

I conducted this study at Chilkat Pass in northwestern British Columbia (59°50'N., 136°35'W.; Appendix 1). The topography, vegetation, and climate of the area are described in Appendix 1. Between 1979 and 1989 approximately 1100 adult willow ptarmigan were marked with numbered aluminium bands as part of a long-term study of willow ptarmigan at Chilkat Pass (Hannon 1983; Hannon 1984; Hannon et al. 1988). The study area was divided into 5 plots: Kelsall Lake (KL), Haines Road (HR), Sprit Mountain (SM), Ridge, and Datlasaka (Hannon 1983, and unpubl.; Appendix 1). HR, Ridge, and Datlasaka plots bordered the highway, whereas the two other plots were 1km or more from the road. Besides willow ptarmigan, Chilkat Pass also supports smaller populations of rock (L. mutus) and white-tailed ptarmigan (L. leucurus) (Weeden 1960), but their densities are not known.

4.2.2 Data collection

From 1987-1990, a hunter check station was set up at the Pleasant Camp Canada Customs station, 55 km south of Chilkat Pass (Appendix 1). The station was operated throughout each hunting season, although in 1987 it was not set up until mid-September, missing the first month of the hunting season. Data could be collected on nearly all hunted birds, as most hunters in the area came from southeast Alaska (pers. obs.). Hunting pressure by Canadians was low, because only a few people live in the area, and hunters from Canadian settlements used other hunting areas that were closer to them. All passing hunters were asked to give one wing from each bird killed, as well as any bands, to Customs officials. Every effort was made to recover bands and wings by informing hunters about the study (Appendix 5). In addition, the number of birds exported per hunting season was collected by the US Fish and Wildlife Service from 1985 to 1989. During the 1979-80 to 1982-83, and 1984-85 to 1986-87 hunting seasons, bands were submitted to customs officials on a voluntary basis. Therefore, a substantial number of bands probably was missed during those years.

I determined the areas used by hunters from my observations and from hunters' own explanations of the areas they used.

4.2.3 Sex and age determination

I determined age of birds by comparing pigmentation on the eighth and ninth primary (Bergerud et al. 1963). I classified birds as chicks from hatch until they finished molting their primaries (approximately October 1). Thereafter I classified them as yearlings until they acquired adult plumage the following autumn. I made this separation as I could not distinguish sex of chicks, whereas this was possible for yearlings. To determine sex of killed birds I used a discriminant analysis. I calculated the discriminant function using the length of the eighth primary and wing chord on a reference collection of 200 birds of known sex, 50 of each sex and age class (Appendix 3).

4.2.4 Data analysis

I divided each hunting season into four 50-day periods. This division gave more accurate results than a division by months, as sample sizes were greater, and not all months were equal in length. The periods coincided approximately with brood rearing (Aug. 15-Oct. 2), winter molt/fall territoriality (Oct. 3-Nov. 21), early winter movements (Nov. 22-Jan. 10), and late winter movements (Jan. 11-Feb. 28), respectively. When comparing sex and age ratios among periods within one hunting season, I excluded the first time period, as I could not determine the age of many birds (because of molting primaries), and I could not distinguish sexes of chicks.

I estimated the percentage of banded birds killed by hunters each year in the following way. First I estimated the number of territorial banded birds present in spring. To this figure I added the birds that were banded that spring and summer, using ptarmigan that were observed at least four times to exclude transient birds. The number of birds available to hunters was lower than the number alive in spring because of natural mortality (Chapter 3). However, because the hunting season extended throughout the winter, it was difficult to determine what percentage of birds was killed naturally before hunting took place. I obtained an estimate of average natural mortality before hunting by subtracting from the number of birds present in spring the number of birds killed naturally between spring and the middle of the hunting season (November 15). From radiotelemetry data (Chapter 3) I concluded that males suffer no mortality during the breeding season, and 35% of overwinter mortality before November. Females suffered approximately 75% of total annual mortality between May and November (Chapter 3). I used the figure thus obtained as the number of banded birds alive during the hunting season.

I compared survival rates of radio-tagged ptarmigan with return of leg-banded birds to determine whether hunting mortality at Chilkat Pass was compensatory. Survival rates were calculated using Kaplan-Meier survival estimates (Pollock et al. 1989; Chapter 3). Return of leg-banded males was defined as the percentage of males counted in spring that returned in a subsequent spring, as breeding season mortality of males is negligible (Chapter 3). For females I used the percentage of females counted after their chicks hatched that returned the following spring. Females that lost their nests were often very secretive, and as a result were easily missed overlooked. Therefore I used only leg-banded and radio-tagged females that successfully hatched chicks in comparing female overwinter survival (Chapter 3). Schieck and Hannon (1989) found that only 10% of males and 31% of females switched territories between years, and 60% of those that switched occupied the neighboring territory. Thus, emigration was not taken into account.

I determined if hunters selectively shot ptarmigan from any one of the plots by comparing the percentage of ptarmigan observed on the plots in the breeding season that were killed the following hunting season. To exclude transient birds, only individuals that were observed at least four times during the breeding season were included.

I compared sex and age ratios with G-Tests of Independence, using Williams' Correction Factor (Sokal and Rolph 1981). When one or more cells contained a value of less than five, I used a G-Randomization Test with 1000 iterations (Sokal and Rolph 1981). In all statistical analyses I considered a difference significant when P was smaller than 0.05.

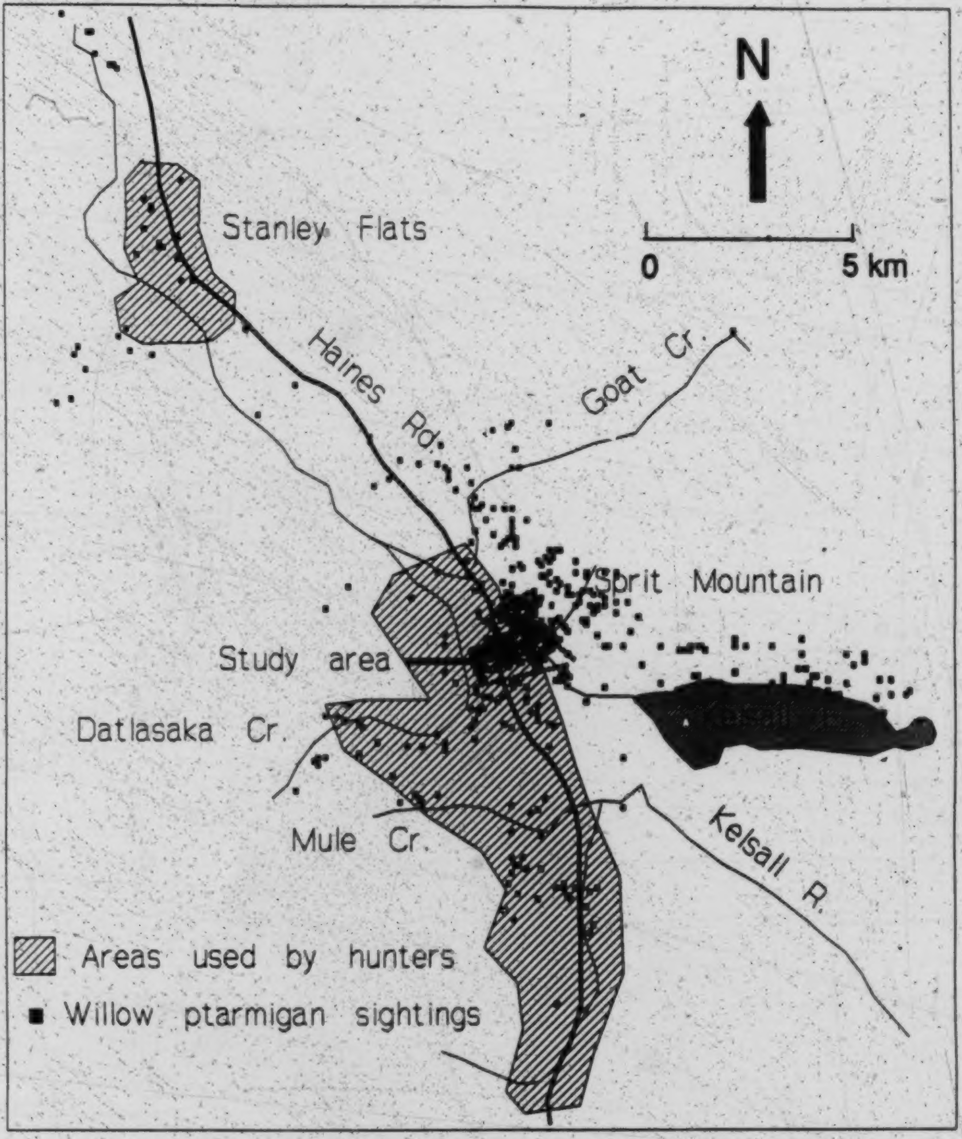
4.3 RESULTS

4.3.1 Annual hunter kill

The total number of wings collected at the check station decreased during the three years of the study, from 691 wings in 1987-88, 647 wings in 1988-89 to 537 wings in 1989-90. During the first 2 years the total numbers of birds exported to Alaska were similar: 653, and 658 for 1987-88 and 1988-89, respectively (export data were not available for 1989-90). The number of exported birds and collected wings were not equal, because not all hunters turned in wings, and hunters who lived at the Canada Customs station did not have to export hunted birds. In 1986-87 797 birds were exported, but in 1985-86 that number was only 225.

Nearly all hunting took place in subalpine habitat (Figure 4-1). Hunting was concentrated in two of the areas where I found radio-tagged ptarmigan during winter 1988-89 (Mule/Datlasaka Creek and Stanley Flats). At Goat Creek and Sprit Mountain I found radio-tagged ptarmigan throughout autumn, and at Kelsall Lake throughout

Figure 4-1 Observations of willow ptarmigan at Chilkat Pass, B.C. September 1987-March 1988, and August 1988-April 1989 (Chapter 2), and areas used by hunters.


N
0
5 km
Stanley Flats
Haines Rd.
Goat Cr.
Sprit Mountain
Study area
Datlasaka Cr.
Mule Cr.
Kelsall R.
▨ Areas used by hunters
■ Willow ptarmigan sightings

winter, but these areas were not used by hunters, because of their relative inaccessibility.

4.3.2 Sex and age composition of hunter kill

During all three hunting seasons significantly more males than females were killed (Table 4-1), but the percentage of males in the hunters' bags differed significantly between hunting seasons (G-Test, G=45.7, df=2, P<0.001). In 1987-88 and 1988-89 similar percentages of males were killed, but in 1989-90 the percentage of males was smaller. In 1987-88 and 1989-90 the sex and age ratio in the hunters' bags changed between time periods, but in 1988-89 the sex and age ratio was not significantly different between time periods (Table 4-1).

The percentage of yearlings among both males and females was significantly different among hunting seasons (Table 4-2; females: G=27.3, df=1, P<0.001; males: G=79.7, df=1, P<0.001). In 1987-88 and 1988-89 half of the females killed were yearlings, and most males were adults, whereas in 1989-90 most males and females killed were yearlings (Table 4-2). However, the percentage of adult females in the hunter bag was similar in all three seasons. In the first two hunting seasons, the percentage of yearlings did not change significantly between periods for either males or females, but in 1989-90 the percentage of yearlings increased significantly among females between periods (Table 4-1).

4.3.3 Hunting mortality of banded birds

In all years less than 20% of banded birds alive were killed by hunters (Table 4-3). Hunting mortality of banded birds did not vary significantly among years (G-Rand. Test; females: G=12.1, P=0.19; males: G=15.3, P=0.07). Nor was there a

Table 4-1 Sex and age ratios of willow ptarmigan killed by hunters by 50-day period, 1987-1990 (percent of kill)

Time Period	Chicks[1]	Males			Females			UK[2]	N
		yrl.	ad.	tot[3].	yrl.	ad.	tot.		
1987-88									
Brood Rearing	0.0	-	66.7	66.7	-	16.7	16.7	16.7	24
Fall Terr.	-	16.0	42.7	58.7	13.3	20.0	33.3	8.0	75
Early Winter	-	24.5	55.9	80.4	7.4	8.0	15.4	4.3	187
Late Winter	-	21.4	47.0	70.3	15.0	10.9	26.9	2.8	313
Total season[4]	0.0	20.8	50.0	71.8^a	11.8	11.3	23.6^a	4.5	600
G (P)[5]	16.4 (0.001)								
1988-89									
Brood Rearing	46.8	-	6.5	6.5	-	20.8	20.8	26.0	77
Fall Terr.	-	17.4	52.2	69.6	8.7	21.7	30.4	0.0	23
Early Winter	-	32.8	46.3	82.1	9.0	7.5	16.5	1.5	67
Late Winter	-	33.2	40.8	75.6	13.3	8.2	21.8	2.5	316
Total season[4]	6.8	28.0	37.2	66.5^a	10.8	9.8	20.8^a	5.9	529
G (P)[5]	7.4 (0.31)								
1989-90									
Brood Rearing	52.0	-	40.0	40.0	-	8.0	8.0	0.0	25
Fall Terr.	-	24.4	34.1	58.5	17.1	19.5	36.6	4.9	41
Early Winter	-	32.6	20.7	54.4	27.2	14.1	41.3	4.4	92
Late Winter	-	37.3	17.5	56.3	31.6	9.9	41.5	2.1	332
Total season[4]	2.6	34.4	19.8	55.4^a	28.5	11.1	39.6^a	2.2	506
G (P)[5]	12.7 (0.004)								

[1] Data from August and first half of September missing.

[2] Birds of unknown sex.

[3] Includes birds of unknown age.

[4] Entire hunting season, includes birds for which it was not known in what period they were killed

[5] G-Test to compare sex and age composition among time periods.

Values with identical superscripts differ significantly at P<0.001 (G-Test)

Table 4-2 Percentage (n) of yearlings among male and female willow ptarmigan in hunters' bags at Chilkat Pass, B.C.

Time Period	Females			Males		
	87-88	88-89	89-90	87-88	88-89	89-90
Brood Rear	-[1]	-	-	-	-	-
Fall Terr	40.0 (25)	28.6 (7)	46[illegible](15)	27.3 (44)	25.0 (16)	41.7(24)
Early Wint	48.3 (29)	54.5 (11)	65.8(38)	30.5(151)	41.5 (53)	61.2(49)
Late Wint	58.0 (81)	61.8 (53)	76.1(138)	31.3(214)	44.9(234)	68.1(182)
Tot.Season[2]	51.1(139)	52.3(109)	72.0(200)	29.4(425)	42.9(345)	63.5(274)
G (P)[3]	2.7(0.26)	2.9(0.25)	5.9(0.005)	0.3(0.87)	2.5(0.28)	6.5(0.004)

[1] Could not distinguish sexes of yearlings (chicks) in August/September

[2] Entire hunting season, includes birds for which it was not known in what period they were killed.

[3] G-Test to compare sex and age composition among time periods.

Table 4-3 **Percentage of banded birds alive that were killed by hunters, 1979-1982 and 1984-1989.**

Year	Females		Males		G[1]	P Value
	% Killed	# Alive	% Killed	# Alive		
1979-80	8.9	34	6.1	49	0.22	0.67
1980-81	7.6	52	10.3	77	0.27	0.64
1981-82	7.0	43	4.6	88	0.32	0.58
1982-83	0.0	14	3.9	51	0.99	0.45
1984-85	18.0	28	7.5	53	1.87	0.21
1985-86	3.2	62	6.8	147	1.14	0.29
1986-87	14.5	97	15.5	161	0.06	0.83
1987-88	6.4	78	10.9	137	1.28	0.30
1988-89	8.2	73	5.9	101	0.34	0.58

[1] G Value from G-Randomization test with 1000 iterations comparing the percentage of killed banded males and females.

significant difference between the percentage of males and females killed in any year (Table 4-3). Because the distance to the road differed among the 5 study plots, hunting mortality may have varied among plots. However, hunters did not selectively shoot birds from certain parts of the study area in any of the years, although there was a trend towards more birds being killed on Ridge and Datlasaka plots in 1987-88 (Table 4-4; sexes combined).

Overwinter survival of radio-tagged ptarmigan was not significantly different from return of leg-banded birds (Table 4-5). Thus, hunting mortality of banded birds appeared to be compensatory. However, sample sizes were small.

In 1987-88 and 1989-90 the percentage of males among banded birds killed by hunters (1987-88: 74% of 31; 1989-90: 71% of 14) was not significantly different from the percentage of males among unbanded adults collected at the check station (1987-88: 81.5% of 368; G=0.93, df=1, P=0.34; 1989-90: 64.1% of 156; G=0.30, df=1, P=0.58). In 1988-89 the percentage of males among banded birds (44% of 9) in hunters' bags was significantly lower than the percentage of males among unbanded adults (79.1% of 249); G=4.95, df=1, P=0.003), but few banded birds were killed that year.

4.4 DISCUSSION

4.4.1 Accuracy of sex determination

The percentage of correctly identified males in the hunter bag was higher than for females (Appendix 3). This was due to differences in feather wear between the reference collection and the hunter-killed sample. Namely, primary 8 was longer in the hunter sample than in the reference collection, and as a result females were more

Table 4-4 Percentage (n) of banded birds observed on different parts of the study area during the breeding season that were killed by hunters, 1979-1982 and 1984-1989.

Year	KL	HR	SM	Ridge	Datlasaka	G^1	P Value
1979-80	4.0(50)	2.6 (38)	-[2]	-	-	0.13	0.74
1980-81	3.0(66)	5.5 (73)	-	-	3.0 (67)	0.74	0.72
1981-82	4.0(50)	5.5 (91)	-	-	5.2 (58)	0.16	0.92
1982-83	0.0(18)	7.7 (26)	-	-	0.0 (32)	4.40	0.10
1984-85	2.7(37)	11.6 (43)		-	9.1 (33)	2.59	0.30
1985-86	0.0(55)	5.9 (85)	2.7 (75)	4.8 (21)	6.1 (66)	6.23	0.26
1986-87	7.7(39)	9.6 (83)	8.7(104)	12.5 (32)	9.7 (93)	0.56	0.97
1987-88	2.8(36)	4.9 (82)	2.5 (81)	8.6 (35)	13.8 (65)	8.88	0.09
1988-89	3.1(32)	4.3 (70)	2.9 (69)	12.5 (32)	1.8 (56)	5.10	0.38
1989-90	3.7(27)	1.3 (78)	0.0 (39)	-	0.0 (40)	2.81	0.52

[1] G Value from G-Randomization test with 1000 iterations comparing the percentage of killed banded ptarmigan from all grids.

[2] Grid not censused in year prior to hunting season.

Table 4-5 Overwinter survival of radio-tagged and leg-banded willow ptarmigan at Chilkat Pass, B.C. during 1987-88 and 1988-89[1]

	Females[2]			Males		
	Surv.	95% C.I.	n	Surv.	95% C.I.	n
1987-88						
Radio-tagged	0.50	0.10-0.90	6	0.65	0.34-0.96	9
leg-banded	0.64	0.48-0.90	22	0.51	0.44-0.58	108
G[3] (P)	0.33 (0.57)			0.80 (0.37)		
1988-89						
Radio-tagged	0.32	0.11-0.53	19	0.43	0.24-0.62	22
Leg-banded	0.42	0.31-0.53	33	0.45	0.36-0.54	51
G (P)	0.59 (0.44)			0.11 (0.74)		

[1] Radio-tagged ptarmigan that were hunted have been excluded.

[2] Females with successful nests only.

[3] Results of G-Test, comparing survival of leg-banded and radio-tagged birds.

often assigned the wrong sex (Appendix 3). Thus, the percentage of females killed by hunters may have been underestimated. At Chilkat Pass, rock ptarmigan cannot be separated readily from willow ptarmigan, because their measurements overlap greatly in this area (Weeden 1959). Rock ptarmigan are slightly smaller than willow ptarmigan, thus their presence in the hunters' bags could result in an overestimate of female willow ptarmigan. However, the number of rock ptarmigan in the area is low compared to willow ptarmigan (Weeden 1959). Therefore, the number of females killed by hunters is probably higher. However, it is difficult to estimate how much higher, as I could test the discriminant function with only 7 known-sex females (Appendix 3).

4.4.2 Sex and age composition of the hunter kill

In 1987-88 and 1988-89 approximately 70% of ptarmigan collected from hunters were males. In 1988-89 80% of male radio-tagged ptarmigan at Chilkat Pass remained in subalpine habitat throughout the winter, in contrast to 33% of females after in December (Chapter 2). Mossop (1987), using recapture data from the same area, found that the percentage of females in subalpine habitat decreases from 40% in November to 10-15% in March. Hunting returns from other populations of willow and rock ptarmigan consisted of between 70 and 80% males in subalpine areas (Weeden 1964; Weeden 1965; Höhn 1984; Gardarsson 1987), whereas in forested regions 80 to 90% were females (Weeden 1964; Höhn 1984; Gardarsson 1987).

In 1987-88 and 1988-89 more adult than yearling males were killed, whereas among females the percentage of yearlings was similar to the percentage of adults. This suggests that most yearling males leave subalpine habitat, as has been found for other populations of ptarmigan (Irving et al. 1967; Braun et al. 1976; Gardarsson

1987). On the other hand, in 1989-90 the percentage of males killed by hunters was only 55%, and more yearlings than adults were killed. That winter very little snow fell (M. Darling, Canada Customs, pers. comm.), and many birds were seen in subalpine areas during the winter (R. Wilson, Yukon Dept. Highways, pers. comm.). As the extent of ptarmigan winter movements is dependent on snow depth (Chapter 2), fewer females and yearlings may have left the subalpine habitat in 1989-90. Mossop (1987) also reported little movement of female willow ptarmigan to forested areas in a year with little snow, although he presented no quantitative data. However, the percentage of adult females was similar in all three seasons, suggesting that they moved to forested areas in 1989-90 despite low snowfall. Yearling female rock and willow ptarmigan move to their wintering grounds later than do adult females (Irving et al. 1967; Myrberget 1975; Gardarsson 1987). Hence, snow depth in 1989-90 could have triggered adult females to move, but not yearlings. Alternatively, more yearlings may have been available as a result of higher chick production the previous summer. In 1990 the density of willow ptarmigan at Chilkat Pass increased, and many yearlings were sighted that spring (S. Hannon, pers. comm.). Thus, the change in age ratios between seasons may have been due to changes in chick production.

During the brood rearing period of 1988-89 and 1989-90, approximately 50% of hunter-killed ptarmigan were chicks, whereas during fall territoriality few young of the year were killed. This difference may be partly due to low sample sizes during both periods. Once they come across a flock of ptarmigan, hunters tend to fill their bag limit from that flock. If sex and age ratios in the flock are skewed (Weeden 1963; Braun and Rogers 1971; Mossop 1987), this will be reflected in the hunters' bag. On the other hand, chicks appear to be more vulnerable than adults to hunting, resulting in biased chick:adult ratios (Bergerud 1970b). Once family groups break up in late

September, young of the year may move with the females farther from the road, and hence suffer less mortality than adult males (see below).

In 1987-88 and 1988-89 more males than females were killed in October and November, even though females did not leave the breeding grounds until December (Chapter 2). Differential movements and behavior probably caused the skewed sex ratio: between late October and early December males were on their territories, while females were found in small flocks 1-3 km from their territories (Chapter 2). Flocks of females tended to be farther from the road than the territories. Weeden (1972) found that in autumn male rock ptarmigan were more likely to be shot than females as males were noisier, and females left subalpine habitat earlier. Male white-tailed ptarmigan are more susceptible to hunting than females in autumn as males are in flocks, which are more easily harvested than females with broods, which are not associated with flocks at that time (Braun and Rogers 1971). In blue grouse more females than males are harvested, since most males leave the breeding grounds, where most hunting is concentrated, prior to the hunting season (Mussehl and Leik 1963; Zwickel 1982).

During the winter of 1988-89 4 of 5 radio-tagged adult females that remained in subalpine habitat throughout the winter were found along Kelsall Lake where no hunting took place, whereas 75% (12 of 16) of radio-tagged adult males in subalpine habitat were in areas frequented by hunters (Mule Creek/Datlasaka Creek and Stanley Flats; Chapter 2). Others have also observed segregation of the sexes of ptarmigan within the same wintering areas (Braun and Rogers 1971; Mossop 1987). Therefore, even within the same habitat males and females may not be equally available to hunters.

At Chilkat Pass most hunters use snowmobiles, and tend to select open areas with hard snow for easy travel. In those areas they may be more likely to come across males than females, as males are more likely to remain close to their territories, and females select more protected habitat (see Chapter 2). Capercaillie (Tetrao urogallus) hunters in Scotland also tend to hunt in open areas, where males predominate (Moss 1987). Yet Moss (1987) used sex ratios from hunters' bags to estimate true sex composition of the population. Clearly, sex and age ratios in hunters' bags do not accurately reflect true sex and age composition, but rather reflect differential movements and behavior of the sexes, and hunters' behavior. With the advent of radio telemetry individual game birds can be followed throughout the year (Chapter 2). This method allows direct examination of sex and age ratios, and of the causes underlying differential movements or mortality. Hence, in the future researchers should refrain from using hunting data for the study of population composition, and initiate radiotelemetry studies to address these questions.

4.4.3 Hunting mortality of banded birds

In 1987-88, there was a trend for hunters to kill banded birds selectively from Ridge and Datlasaka plots, which lie adjacent to the road. In that year more hunting took place in autumn than in other years. In autumn 1985 and 1988 3 of 5 and 4 of 8 radio-tagged birds from Datlasaka and Ridge respectively, remained on their territories, whereas on HR plot, which also borders the highway, 9 of 11 radio-tagged bird left their territories in autumn and moved uphill, away from the road (Chapter 2). Hence, in years with high autumn hunting pressure there may be differential mortality among the plots. Fisher and Keith (1974) also reported that hunting pressure on ruffed grouse (Bonasa umbellus) decreased with increasing distance from banding location to the nearest road.

In none of the years was hunting mortality of banded males and females significantly different. The difference in sex ratios between banded and unbanded ptarmigan may have been due to the timing of hunting. Most hunting on the study area (where ptarmigan were banded) took place during brood rearing, when males and females were still together, whereas most unbanded birds were killed in winter, after the sexes had segregated.

The total annual hunting mortality of banded adult birds was less than 20% in all years, which is one half of natural autumn and winter mortality (Chapter 3). Natural overwinter mortality of radio-tagged birds was not significantly different from mortality (natural and hunting) of leg-banded birds. This suggests that, as transmitters do not appear to affect predation rates (Chapter 3), hunting mortality is compensatory. However, sample sizes of radio-tagged birds were small. Myrberget (1985) argued that some hunting must be compensatory, but he could not determine what percentage. He concluded that moderate hunting should be possible without long-term effects on the population. Others concluded that grouse can sustain a hunting pressure of up to 30-40% (Braun and Rogers 1971; McGowan 1975; Ellison 1979). However, these rates were based on data from populations that were hunted during a shorter time in autumn, before the period of highest natural mortality. At Chilkat Pass, most hunting takes place in late winter, during and after the periods of highest natural overwinter mortality (Chapter 3). As a result, natural mortality cannot compensate for hunting mortality. Thus, in areas where the hunting season extends into late winter or spring, and most hunting takes place towards the end of the season, populations may not be able to sustain as high a hunting mortality as populations with only an autumn hunting season.

Although hunting mortality of banded birds appeared low in comparison to natural overwinter mortality, the percentage of banded birds killed at Chilkat Pass may not represent average exploitation for the entire valley, because in the areas of most frequent hunting resident birds were not banded. Thus, exploitation of the total area may be much higher, especially locally, but from the present data I cannot calculate a total exploitation level. Moreover, it is not known what percentage of the population is wounded and becomes more vulnerable to predation as a result, although Mercer (1967) estimated that crippling losses were less than 27 percent of total hunter kill in Newfoundland willow ptarmigan. It has been argued that if the hunting area is small, immigration of yearlings from nearby areas should compensate for hunting mortality (Mercer 1967; Bergerud and Huxter 1969; Myrberget 1985; Lindén 1981). At Chilkat Pass, hunting was not equally heavy in all wintering areas. Hence, immigration from less heavily exploited areas may compensate for high local losses.

Numbers of willow ptarmigan at Chilkat Pass fluctuate with a periodicity of 8-11 years (Mossop 1987). During the study densities were low (S.J. Hannon, pers. comm.). When densities are high the number of hunter-killed birds may increase, as they would be easier to find. This may explain the high number of hunter-killed birds in the late seventies, when ptarmigan densities were high, and lower hunting pressure in 1985-86 when densities were low. Although my data showed no change in the percentage of banded birds in different stages of the cycle, the percentage of unbanded ptarmigan killed by hunters is likely to vary. The percentage may well be highest during low densities, and lower when densities are high. However, this will depend on hunter effort during the different stages of the cycle.

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CHAPTER 5 THESIS DISCUSSION

Differential mortality of the sexes has been reported in willow ptarmigan (Lagopus lagopus) (Martin 1985; Hannon and Barry 1986; Chapter 3), Franklin's spruce grouse (Canachitis canadensis franklinii) (Boag et al. 1979), blue grouse (Dendrapagus obscurus) (Zwickel et al. 1983), and black grouse (Tetrao tetrix) (Angelstam 1984). There are two possible causes of this phenomenon: either the sexes segregate outside the breeding season (Weeden 1964; Hoffman and Braun 1975; Höhn 1984; Mossop 1987), and as a result are exposed to different environmental conditions, and/or different predation pressure, or differences in reproductive demands between males and females may cause differential risk to predation during the breeding season (Clutton-Brock et al. 1982).

Once willow ptarmigan at Chilkat Pass left the breeding grounds in December, males and females segregated (Chapter 2), similar to other ptarmigan (Weeden 1964; Hoffman and Braun 1975; Gardarsson 1987; Mossop 1987). Males remained close to the breeding grounds, whereas females moved farther to the boreal forest. However, the sexes suffered similar mortality from predation throughout autumn and winter (Chapter 3). Moreover, there appeared to be no difference in mortality between birds that remained in subalpine habitat and those that moved to the boreal forest, although sample sizes were small (Chapter 3).

Nearly all hunting at Chilkat Pass took place in subalpine habitat. As a result, among unbanded ptarmigan more males than females were killed. Even in a winter with little snow, males predominated in hunters' bags (Chapter 4). Hunting mortality of banded birds was low in comparison with natural mortality, and banded males and females suffered similar hunting losses (Chapter 4), but in areas with higher hunting pressure, males may well suffer higher mortality.

On the other hand, females suffered higher mortality than males during the breeding season, although the sexes were found together on their territories. Thus, during my study, differential mortality took place during the breeding season as a result of risks associated with incubation and chick rearing for females, rather than because of segregation of the sexes outside the breeding season. Variation in breeding season mortality was caused by changes in levels of red fox (Vulpes vulpes) predation. Foxes may have switched to ptarmigan when small mammals were scarce (Chapter 3).

Numbers of ptarmigan based on spring counts have remained stable since 1985 throughout the Coast Mountains of northwestern British Columbia, whereas to the north in the Yukon they have increased since then (S. J. Hannon pers. comm.; D.H. Mossop, pers. comm.). Only in 1990 did numbers of ptarmigan at Chilkat Pass increase (S. Hannon, pers.comm.). This delayed increase may have been caused by increased predation on females during the breeding season as a result of low numbers of small mammals from 1987 until 1989. In Scandinavia, absence of vole cycles at more southern latitudes is thought to be due to higher levels of predation on voles (Angelstam et al. 1987). Hence, predation during the breeding season may contribute to determining breeding densities of willow ptarmigan at Chilkat Pass.

Although segregation of the sexes outside the breeding season did not cause differential mortality of the sexes during my study, it may play a role in other years. During winter, foxes were probably the major predator of males, whereas females were probably subjected to higher predation by raptors (Chapter 3). Hence, the number of foxes, and possibly gyrfalcons (Falco rusticolus), determine male winter mortality, whereas female winter mortality is more likely tied to raptor numbers in the boreal forest. During the study, numbers of snowshoe hares (Lepus americanus) were increasing (Appendix 4). Thus, predators probably concentrated on killing the more numerous hares. Once hare numbers crash, however, they may well switch to ptarmigan (Keith and Rusch 1986; Chapter 3; see Hörnfeldt 1978; Angelstam et al. 1984). Although snowshoe hares occurred both in male and female wintering areas (Appendix 4), they were probably more numerous in the boreal forest. Within the forest, hare densities were also variable: they were lower at the forest edge than at Kluane Lake, 100km to the northwest (Appendix 4). In areas with higher hare densities predators can also be expected to be more numerous. Thus, females, which moved as far as 60km past the edge of the forest, would be more likely to be taken by predators switching from hares. However, the extent of ptarmigan winter movements is determined by snow fall (Chapter 2). As a result, the degree of differential mortality in winter during the decline of hare numbers is partly dependent on winter weather, although some forest-dwelling predators may move to subalpine habitats.

Movements of willow ptarmigan during autumn and winter appeared to be governed by predation risk. In fall, ptarmigan were most vulnerable to predation during raptor migration, which also coincided with the brood rearing period, as well as during molt into winter plumage (Chapter 3). Ptarmigan moved to areas of greater cover during these periods, most likely to reduce the risk of predation. It appeared that during brood rearing at Chilkat Pass only birds from territories in areas with less vegetative cover and lower vegetation height moved to denser vegetation uphill from their territories (Chapter 2). After winter molt was completed, all males, but only half of the females returned to their territories, which resulted in a partial segregation within the same area (Chapter 2). Hunting records also suggested that segregation of the sexes occurred on the breeding grounds in autumn, as males dominated hunters' bags in late autumn, even though females had not yet left the area (Chapter 4).

Segregation within subalpine habitat may cause differential mortality of males in areas with high hunting pressure if males are more accessible than females.

Molted ptarmigan only returned to their territories when the breeding grounds were snow covered, presumably because they then matched their background, and were less conspicuous (Chapter 2). Once they were on their territories, male ptarmigan appeared relatively safe from predators, as predation rates on males were low then (Chapter 3). Males displayed actively throughout the period they were on their territories, but only at dawn and dusk (Chapter 2), most likely to minimize predation risk (Pedersen et al. 1983). Meanwhile, most females remained in small flocks within 3km of their territories (Chapter 2), and also suffered little mortality (Chapter 3). Ptarmigan remained on or near their territories as long as possible in autumn, and only moved to wintering grounds when a combination of snow depth and wind depleted cover and food (Chapter 2). Thus, in the absence of snow, willow ptarmigan would remain on or near the breeding grounds throughout the winter, as Mossop (1987) observed. A similar distribution also occurs in red grouse (Jenkins et al. 1963), and rock ptarmigan during mild winters (Bossert 1980).

In spring, males returned to their territories on approximately the same date both years, despite differences in snow depth, and hence available cover. I found no depredated males on their territories, which suggests that males are relatively safe to predators while on their territories (Chapter 3). However, they moved to more protected areas during periods of bad weather, and sometimes during the day, presumably to feed and seek cover (Chapter 2). Males were killed in those areas or while in transit (Chapter 3). Similar to movements from the breeding grounds in winter, spring movements to and from territory depend on the amount of available cover, which in turn is related to the amount of snow that fell during winter, and the frequency of spring storms (Chapter 2). Thus, mortality of males during spring may be tied to weather conditions. Females, on the other hand, returned to their territories later than males, and even those that returned early left again, and congregated in small flocks nearby (Chapter 2). During that period no females were killed.

My data suggest that the presence of a mate did not decrease vulnerability of females with broods to predation. Neither did males that accompanied females with broods suffer higher mortality than males not accompanying broods. Martin and Cooke (1987) also observed that widowed and paired females had similar return rates in subsequent years. They suggested that bi-parental care in willow ptarmigan developed as strategy by males to ensure paternity in re-nesting attempts, and to reduce loss of fitness if their mate died. However, male willow ptarmigan remain with their mates and brood until September (Wittenberger 1978; Chapter 2), well after the re-nesting period. Hence, paternity in re-nesting attempts cannot be the sole reason for male parental care in willow ptarmigan.

Unlike willow ptarmigan, most male rock and white-tailed ptarmigan leave before hatch (MacDonald 1970; Schmidt 1987). They congregate into small flocks uphill from the breeding areas (Bossert 1980; Schmidt 1987). Rock and white-tailed ptarmigan tend to occur at lower densities than willow ptarmigan (e.g. Braun and Rogers 1971; Gardarsson 1987; Hannon and Gruys 1987; Mossop 1987), and especially white-tailed ptarmigan suffer low annual mortality (Braun and Rogers 1971). Jenkins et al. (1964) argued that vulnerability of prey affects behavior and hence distribution of predators, rather than the reverse. Hence, because of low prey densities and possibly also because of habitat characteristics (e.g. boulder fields, frequent fog (Bergerud 1987)) rock and especially white-tailed ptarmigan escape predation. In contrast, many willow ptarmigan with a larger number of chicks are available to predators in the lower parts of the valleys (see also Bergerud 1987). Consequently, willow ptarmigan have a higher risk of predation in fall than rock or white-tailed ptarmigan. By remaining with the female until September, willow ptarmigan males invest more energy into raising their offspring than rock or white-tailed ptarmigan males. Therefore, willow ptarmigan males must benefit to offset the additional energy investment. Hannon and Martin (1991) suggest that males remain with the female to raise the brood if the female dies ("salvage strategy"). I suggest that post-fledge male parental care not only allows the male to raise its offspring if the female dies but also increases the chances of survival of the female and the brood. Among ptarmigan the benefits of male parental care after chicks have fledged apparently only outweigh the costs in willow ptarmigan. Further studies on autumn survival of all three species of ptarmigan are needed to explain the differences in male parental care between the species.

In conclusion, overwinter mortality of willow ptarmigan is closely related to their movements, which in turn are regulated by weather patterns. Differences in environmental conditions, then, explain variations in winter movement and mortality patterns between ptarmigan and other grouse, but also among populations of ptarmigan, and among years within the same population of ptarmigan. When ptarmigan are segregated within the same area, or are close together on their territories, they are exposed to similar environmental conditions, but yet may suffer differential mortality as a result of differences in reproductive demands, or variation in access for hunters. Although mortality plays an important role in the dynamics of both male and female ptarmigan populations, the level of mortality may differ between the sexes at any time of the year as a result of environmental variables and population dynamics of other prey species. These factors, then, may account for many of the differences in movements and mortality observed among grouse species, populations of ptarmigan, or years within populations.

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6 APPENDIX 1 DESCRIPTION OF THE STUDY AREA

6.1 Topography and vegetation

The study area was located at Chilkat Pass in northwestern British Columbia (59°50'N., 136°35'W.; Figure 6-1). Ptarmigan breed on a large plain ("Datlasaka Flats"; elev. 890m), that separates the Chilkat and Tatshenshini watersheds (Figure 6-2). The Datlasaka Flats are flanked by the Coast Mountains in the east, and the St. Elias Mountains in the west, each with peaks reaching 2300m In the eastern half of the flats lies a large glacial lake, Kelsall Lake, while the remainder of the flats is comprised of the flood plain of Datlasaka Creek. This flood plain extends from the western edge east and northward around a moraine which bisects the flats. Vegetation on the flood plain is dominated by willow (Salix spp.) and dwarf birch (Betula glandulosa; Weeden 1960) reaching a height of 1.5m. On the mountain slopes dense stands of willows and birch of up to 2.5m tall dominate the vegetation, with patches of alder (Alnus spp.) as tall as 3m at higher elevations. The shrubs are interspersed with ponds and wet meadows which are dominated by graminoids, bryoids, and perennial forbs (Weeden 1960). In July, these species form a thick mat of vegetation, reaching its greatest height in August, when ground vegetation can be 1m or taller. Above approximately 1100m a.s.l. vegetation is dominated by heaths (Cassiope spp., Phyllodoce spp.), dwarf willows, saxifrage (Saxifraga spp.), Vaccinium spp., Crowberry (Empetrum nigrum), lichens, and mosses (Weeden 1960). At this elevation slopes are steep, and many boulder fields occur (Weeden 1959). White spruce (Picea glauca), reaching a height of 5-6m, occurs on the southern fringe of the flats as well as along the southern shore of Kelsall Lake. Several stands of aspen

Figure 6-1 Map of Chilkat Pass, B.C. and surrounding areas.

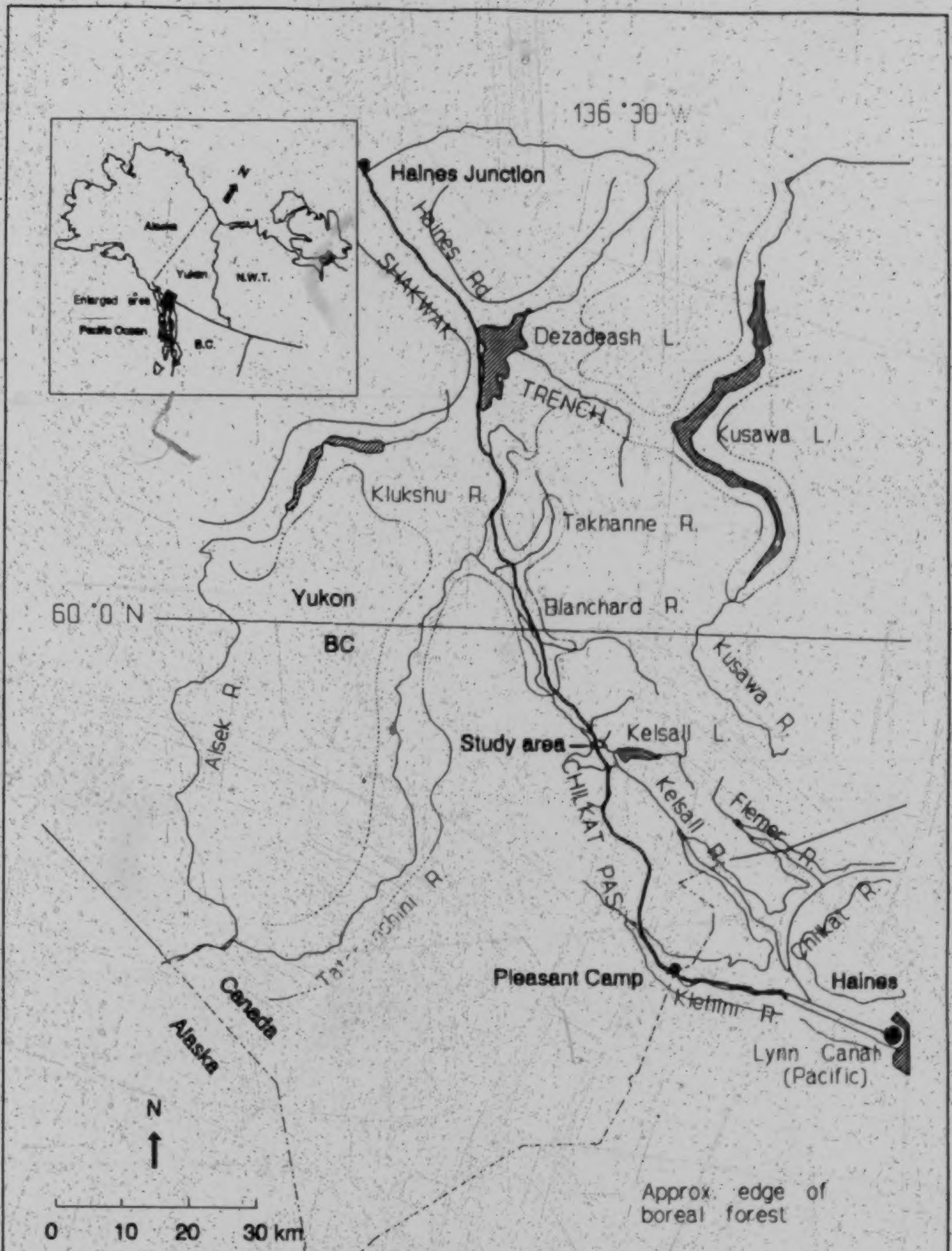
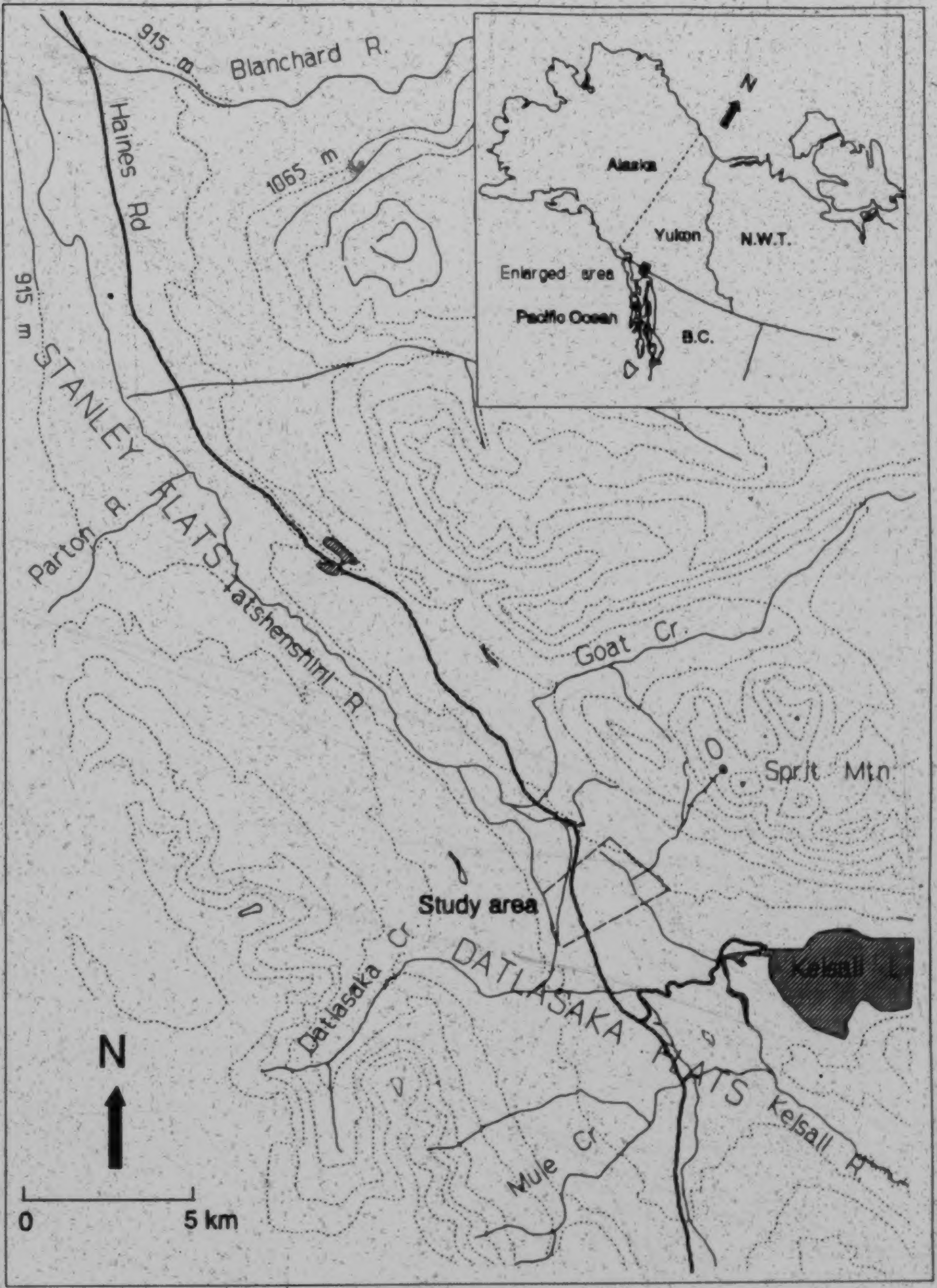
136 °30 'W
Haines Junction
Haines Rd
SHAKWAK
TRENCH
Dezadeash L.
Kusawa L.
Klukshu R.
Takhanne R.
Blanchard R.
60 °0 'N
Yukon
BC
Kusawa R.
Alsek R.
Study area
Kelsall L.
CHILKAT PASS
Kelsall R.
Klehini R.
Flemer R.
Chilkat R.
Tatshenshini R.
Pleasant Camp
Haines
Lynn Canal
(Pacific)
Canada
Alaska
N
0
10
20
30 km
Approx. edge of boreal forest
Alaska
Yukon
N.W.T.
Enlarged area
Pacific Ocean
B.C.
N

Figure 6-2 Map of study area at Chilkat Pass, B.C.


915 m
Blanchard R.
1065 m
Haines Rd
915 m
STANLEY FLATS
Parton R.
Tatshenshini R.
Goat Cr.
Spirit Mtn
Study area
Kelsall L.
Datlasaka Cr.
DATLASAKA FLATS
Kelsall R.
Mule Cr.
N
0
5 km
N
Alaska
Yukon
N.W.T.
Enlarged area
Pacific Ocean
B.C.

(Populus tremuloides) of up to 7m tall are present along the northern shore of Kelsall Lake.

On the Pacific side of Datlasaka Flats the Kelsall River valley descends abruptly into a narrow valley covered by coastal forest, with a dense cover of willow and alder at higher elevations (Weeden 1959). This valley gives access to the Pacific Ocean, 90km from Datlasaka Flats. Two other valleys connect Datlasaka Flats to the Pacific: the Flemer River in the east and the Klehini River in the west.

From the northern fringe of Datlasaka Flats the Tatshenshini River flows in a northwesterly direction through a second basin ("Stanley Flats"), which lies at 860m a.s.l. The central section of Stanley Flats comprises the flood plains of Parton River and Stanley Creek, and like Datlasaka Flats is poorly drained. However, the perimeter of Stanley Flats is covered by an open-canopy white spruce forest, interspersed with willow and birch. At the northern edge of Stanley Flats the Tatshenshini River drops into a deep gorge which is flanked by gradually sloping, forested benches. Approximately 20km further north the gorge widens into a broad valley which connects to the Klukshu and Takhanne River valleys. Vegetation in the valleys north of Stanley Flats is dominated at lower elevations by spruce with stands of aspen. Above the treeline lies a narrow band of willow and birch below steep rock slopes. The Klukshu and Takhanne River valleys both give access to Dezadeash Lake, where the Chilkat Pass connects to the Shakwak Trench. This broad valley extends from Kusawa Lake in the southeast to Haines Junction and the Kluane Lake region in the northwest.

6.2 Study site

Ptarmigan have been studied intensively on a 4.5km² site in the northwestern corner of Datlasaka Flats and lower slopes of Sprit Mountain since 1979 (Hannon et al. 1988). The site is divided into five plots; Haines Road, Sprit Mountain, Kelsall Lake, Ridge, and Datlasaka (Figure 6-3). Each plot has been divided into 100x100m squares by means of permanent grid stakes (Hannon 1983).

6.3 Weather

The Chilkat Pass forms a nearly straight corridor linking the Pacific Ocean to the Yukon Territory. Hence, weather at Chilkat Pass is influenced both by moist Pacific and dry Yukon air. The Pacific air causes much precipitation, especially in early spring and autumn. The recorded average annual precipitation is 710 mm[1], of which 360 mm falls as snow. The first snow can fall as early as September, but usually does not remain on the ground before late October. During most winters snow depth reaches approximately 1 to 1.5m. Snow usually starts to melt in late April and has disappeared from all but the mountain peaks by late May. The influence of the Pacific Ocean decreases as one moves northward towards the Yukon. At Dezadeash Lake, 60km north of Datlasaka Flats, average annual precipitation is 340 mm (average 1975-1984), of which 170 mm falls as snow. Because of the straightness of the Chilkat Pass corridor, air can flow through it relatively unhindered. This results in high winds in the centre of the valley, whereas the side valleys are more protected.

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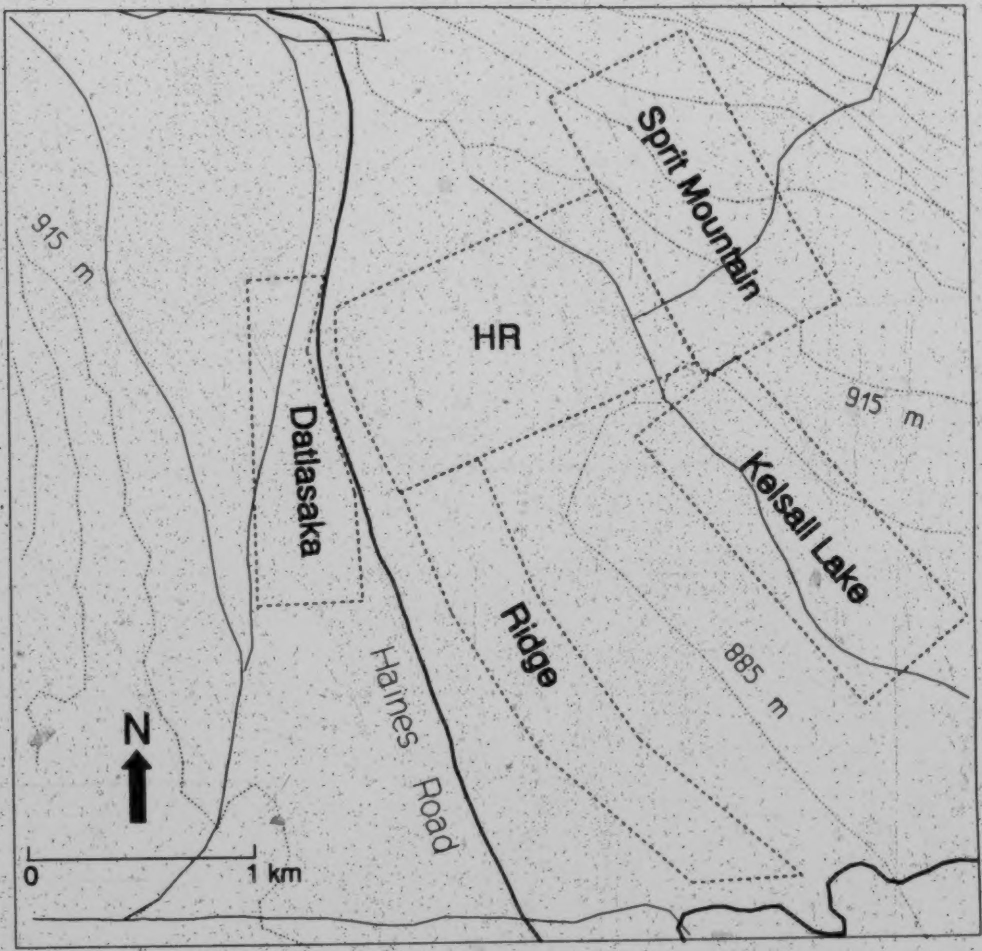
[1] Official average from 1971 until 1985 at Mule Creek Highway Maintenance Camp (59°47'N, 136°36'W). However, because of strong winds during winter much snowfall was not recorded (R. Wilson, Yukon Dept. Highways, pers. comm.). Thus the true average is higher.

Figure 6-3 Map of study site at Chilkat Pass, B.C., indicating study plots with permanent reference grids.



Sprit Mountain
HR
915 m
915 m
Datlasaka
Kelsall Lake
Ridge
885 m
Haines Road
N
0
1 km

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7 APPENDIX 2 RADIO TELEMETRY METHODS USED IN THE STUDY

7.1 Radio collars

In July of 1987, I equipped nine territorial males and nine resident females with 18g, 3.5V two-stage radio transmitters (Austec, Edmonton, Alta), which had a life expectancy of up to five months. They were attached to the bird using a necklace made of nine kg steel trolling line inside thin-walled hollow PVC tubing. Range of these transmitters was approximately 1.5km on flat terrain. In July of 1988, I equipped 23 territorial males and 26 resident females with transmitters with a battery life of one year. To 42 of these birds I attached 15g transmitters (Biotrack, Wareham, Dorset, UK), to five birds 21g transmitters (Telemetry Systems, Mequon, WI), and to two birds 25g transmitters (Telemetry Systems). Tags of the first category were attached with a necklace made of soft cord (Kenward 1987), and those of the latter two categories with a necklace made of harness wire as described above. Range of the Biotrack transmitters was approximately one km on flat terrain, while the other two designs had a range of approximately two km on flat terrain.

7.2 Telemetry

I tracked radio-tagged ptarmigan with Telonics (Mesa, AZ), Austec (Edmonton, AB), and LA-12 (AVM Instrument Co., Livermore, CA) receivers, and three-element, hand-held Yagi antennas (AF Antronics, White Heath IL). In 1988-89 I also located radio-tagged ptarmigan by triangulation using a truck-mounted, removable null-dipole antenna, modified after Hallberg et al. (1974). The array consisted of two three-element Yagi antennas (AF Antronics), spaced exactly one wavelength (2m) apart on a wooden crossbeam. The crossbeam was attached to a 2.5m aluminium television mast, which could turn freely in a tripod mount by means of a ball bearing assembly. The mast was stabilized using six-strand, high-strength stainless steel guy wires attached to a ball-bearing below the crossbeam. This construction was strong enough to permit use of the antenna in very high winds, and allowed the truck to be driven at normal speeds on paved roads. Because the mast, guy wires, and the truck caused considerable magnetic deflection, the antenna was oriented with a Thommen H-104 prismatic compass (Revue Thommen, Waldenburg, Switzerland; accuracy ±0.1°) by taking a bearing of the antenna from 20m while the antenna was locked in place at 360°. Bearings were read from a compass card attached to the mast and added to the compass bearing. Accuracy of this method was ±1°. I calculated the locations of radio-tagged birds with Andrew's estimator (Lenth 1981) and checked each location graphically by computer (program TRIANG; White and Garrott 1990).

7.3 Coordinate systems

All locations of birds on the intensive study site were recorded in terms of the permanent grid markers on the site. I calculated the position of these grids in relation to the Universal Transverse Mercator (UTM) grid by triangulating transmitters located at 33 grid stakes. Locations of birds on the permanent grids were converted to UTM-coordinates by calculating the distance to the nearest one of the 33 reference stakes. Because of the scarcity of UTM reference stations in the area, and the error in the triangulation method, these UTM-coordinates had ±50m accuracy.

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8 APPENDIX 3 METHODS FOR SEX DETERMINATION OF WILLOW PTARMIGAN AT CHILKAT PASS, B.C.

8.1 INTRODUCTION

In order to assess the relative impacts of hunting and predation on the sexes, it is necessary to be able to determine the sex of dead birds. Techniques used to determine sex of live birds (e.g. plumage color and pattern, series of morphological measurements) may not be applicable in sex determination of hunted or depredated birds. Remains may be limited to a single wing or a few feathers, and in species like ptarmigan (Lagopus spp.), plumage color is not diagnostic in winter and early spring.

Bergerud et al. (1963), and West et al. (1968) presented a method for sex determination of willow ptarmigan (L. lagopus) in Newfoundland and Alaska respectively, based on wing and rectrix length. However, this technique has not been useful for all subspecies because of size differences (e.g., West et al. 1970; Voronin 1971; pers. obs.). Myrberget et al. (1969) determined sex correctly for 93 percent of Norwegian ptarmigan using a regression of wing length on length of the outer rectrix. However, they suggested examining internal sex organs when there was overlap between the sexes.

Mean rectrix and wing length differed significantly among sex and age classes in Colorado white-tailed ptarmigan (L. leucurus), but because of a great overlap in the observed ranges and tolerance limits, specimens could not be correctly classified (Braun and Rogers 1971). Sexes of rock ptarmigan (L. mutus) can be separated using presence or absence of black lores (Myrberget et al. 1969), although Nielsen (1986) measured the length of the humerus to determine sex in Icelandic rock ptarmigan, and found that males had significantly longer humeri than females. Poole (1987) obtained similar results in Canadian rock ptarmigan, but observed great overlap between the sexes. In many depredated birds the humerus is often broken or absent, and it is difficult to obtain from hunted birds. Thus this is not a useful technique.

In the present study I hoped to find a satisfactory separation between male and female willow ptarmigan at Chilkat Pass using morphological measurements which could easily be obtained from wings collected from hunters, as well as from remains of depredated birds.

8.2 METHODS

8.2.1 Nomenclature

Several terms have been used for sub-adult ptarmigan. Bergerud et al. (1963) refer to young of the year as chicks before, and juveniles after autumn molt, whereas Mossop (1987) uses both yearling and juvenile for young of the year during their first winter, and Hannon (1984) refers to birds which had survived one winter as yearlings. I will refer to young of the year as juveniles or chicks until they have molted into autumn plumage, which they acquire by October 1 (Bergerud et al. 1963). Thereafter I will refer to them as yearlings until the following autumn, when they obtain adult plumage.

8.2.2 Measurements and data analysis

I conducted this study at Chilkat Pass in the northwestern part of British Columbia (59°50'N., 136°35'W.). To obtain a reference collection, 200 willow ptarmigan of known sex and age, 50 from each age and sex class, were captured (Hannon 1983) during April and May, and wing chord was measured. The eighth and ninth primaries (counting distally), and both outer rectrices were pulled. Length of the primaries and longest rectrix were measured in the laboratory to the closest mm by one person. Specimens with missing measurements were excluded from analysis. Sexes were distinguished on the basis of plumage and voice (Bergerud et al. 1963). Age was determined in the field from pigmentation on the eighth and ninth primary (Bergerud et al. 1963). Wing chord was taken on an unflattened wing from the outside bend of the carpal joint to the tip of the longest primary on the folded wing (Bergerud et al. 1963). Primaries and rectrices were measured from the beginning of the vane to the tip of the feather. Others measured these feathers to their point of insertion (West et al. 1968), or the plucked feather (Bergerud, in West et al. 1968), but these methods were not acceptable for my study, as mammalian predators usually bit off the feathers above the point of insertion. I used rectrix 1 as it can be easily distinguished from other rectrices by its vane, which is more asymmetrical than that of others (Bergerud et al. 1963). This is especially useful when studying prey remains, as rectrices are often shed.

The specimens were separated into groups on the basis of sex and age. Mean, range, standard deviation, and 95% confidence intervals were calculated for each measurement. An ANOVA was carried out to determine if the differences in mean length of each measurement between sex and age groups were significant. As there was overlap on all measurements between groups, I tried to determine if a reliable separation between sexes could be found by performing discriminant analyses (Gnanadesikan 1977; Kleinbaum and Kupper 1978) incorporating different sets of measurements. To determine which measurements to use in the analyses, I first ran a stepwise multiple regression on the complete sample to determine which measurements added significantly to the function. Alpha-to-remove was set to 0.05 and alpha-to-add to 0.10 (Sokal and Rolph 1981).

To test the accuracy of the discriminant analyses I randomly divided the reference collection into two, and used one half to calculate the discriminant functions, and the other half to calculate the percentage of birds identified correctly with each function. I repeated the calculations after dividing the collection in a different random manner, and calculated the average percentage of correctly identified birds. I then used the entire reference collection to calculate the discriminant function, and tested its accuracy on known-sex depredated and hunter-killed birds of known sex collected at Chilkat Pass.

8.3 RESULTS

The descriptive statistics for each measurement of birds in the reference collection are shown in Table 8-1. The difference in wing chord between age groups was not significant in either sex (Table 8-2). Moreover, in females there was no significant difference in the length of primary 8 between yearlings and adults. Therefore, division of age groups into yearlings and adults improved the separation between sexes for all measurements except wing chord, and primary 8 for females. For yearlings the difference in mean lengths between sexes was significant for all measurements (Table 8-2), but the range of measurements showed overlap (Table 8-1). In adults the difference between sexes in mean lengths was significant for all measurements except wing chord, but the ranges also indicated overlap. Thus, it was impossible to distinguish between sexes using only one measurement.

When all four measurements were available, only wing chord and rectrix length added significantly to the multiple regression function. When primaries 8, and 9 and

Table 8-1 **Comparison of descriptive statistics from wing and tail measurements between sex and age groups of willow ptarmigan at Chilkat Pass, B.C.**

	Yearlings		Adults	
	Females	Males	Females	Males
Wing chord				
Sample size	49	50	48	49
Mean (mm)	179.0	189.3	179.2	189.8
Range	169.0-192.0	176.0-200.0	167.0-192.0	177.0-200.0
Standard Dev.	4.48	5.21	5.91	5.70
95% conf. lim.	177.7-180.3	187.8-190.7	177.5-180.9	188.1-191.4
Primary 9				
Sample size	50	50	49	50
Mean (mm)	116.1	121.3	119.4	126.3
Range	110.0-124.0	112.0-129.0	111.0-128.0	120.0-136.0
Standard Dev.	3.21	3.79	4.22	3.94
95% conf. lim.	115.2-117.0	120.2-122.3	118.2-120.7	125.2-127.4
Primary 8				
Sample size	50	50	49	50
Mean (mm)	121.0	127.1	122.1	129.0
Range	113.0-128.0	120.0-133.0	115.0-131.0	120.0-138.0
Standard Dev.	3.29	3.29	3.74	3.70
95% conf. lim.	120.1-122.0	126.2-128.1	121.0-123.2	128.0-130.1
Rectrix 1				
Sample size	50	50	49	50
Mean (mm)	97.2	105.3	100.4	110.9
Range	88.0-106.0	96.0-116.0	80.0-118.0	95.0-120.0
Standard Dev.	4.43	4.28	5.81	4.88
95% conf. lim.	95.9-98.5	104.1-106.6	98.7-102.1	109.5-112.3

Table 8-2 P values from comparisons of means of wing and tail measurements between sex and age groups, using a single classification ANOVA

	Between sexes		Between ages	
	Juveniles	Adults	Females	Males
Wing chord	P<0.001	P=0.056	P=0.986	P=0.405
Primary 9	P<0.001	P<0.001	P<0.001	P<0.001
Primary 8	P<0.001	P<0.001	P=0.129	P=0.008
Rectrix 1	P<0.001	P<0.001	P=0.009	P<0.001

wing chord were available, only wing chord and primary 8 added significantly to the function. When rectrix length, and primaries 8 and 9 were available, only rectrix length and primary 8 added significantly to the function. In the discriminant analysis, the model which incorporated both wing chord and rectrix length provided the greatest separation between the sexes (Table 8-3). However, it was not possible to obtain both wing and tail feathers from hunter-killed birds, and wing chord could often not be measured in depredated birds. A discriminant analysis using models which incorporated only wing chord and primary 8, or rectrix length and primary 8 resulted in a slightly poorer separation (Table 8-3). Division into age classes provided better results when rectrix length could be measured, but this was not the case when wing chord and primary 8 were used.

When depredated birds of known sex were used to test the discriminant function based on primary 8 and wing chord or rectrix length, the percentage of correctly classified females was higher than when the reference collection was used, whereas the percentage of correctly classified males was lower. However, among hunter-killed birds, females were more often misclassified than females of the reference collection, whereas hunter-killed males were nearly always classified correctly (Table 8-3). These differences in misclassified birds were caused by differences in feather lengths between groups: depredated birds had significantly shorter rectrices than birds in the reference collection, while among hunter-killed birds primary 8 was significantly longer than in the reference collection (Table 8-4).

Table 8-3 Percentage of willow ptarmigan classified correctly to sex, using a discriminant analysis incorporating different sets of measurements

a. Reference collection

	Females (n)	Males (n)	Average
Wing, R1			
Juveniles	89.6 (24)	90.0 (25)	89.8
Adults	92.0 (24)	82.0 (25)	87.0
P8, Wing			
Juveniles	88.8 (24)	84.0 (25)	86.4
Adults	86.0 (25)	84.0 (25)	85.0
Ages combined	88.7 (49)	86.0 (50)	87.4
P8, R1			
Juveniles	80.0 (25)	90.0 (25)	85.0
Adults	88.0 (25)	82.0 (25)	85.0
Ages combined	84.0 (50)	84.0 (50)	84.0

b. Known-sex depredated and hunted birds

	Females (n)	Males(n)	Average
Wing, R1	-[1]	-	-
P8, Wing[2]			
Hunted	57 (7)	100 (17)	94
Depredated	100 (5)	75 (4)	88
P8, R1			
Depredated	87 (15)	71 (7)	79

[1] Insufficient data.

[2] All banded birds were adults.

Table 8-4 **Comparison of average measurements between a reference collection and known-sex hunter-killed and depredated willow ptarmigan (all measurements in mm)**

	Primary 8		Wing length		Rectrix 1	
	Female	Male	Female	Male	Female	Male
Reference coll.	122.1[a]	129.0[a]	179.2	189.8	100.4[b]	110.9[a]
Hunted	125.0[a]	134.1[a]	178.8	191.7	-	-
Depredated	121.0	128.4	176.2	190.0	97.8[b]	107.7[a]

Within each column, numbers followed by [a] are significantly different at alpha=[illegible]05 (t-Test). Numbers followed by [b] are significantly different at alpha=0.05 (approximate t-Test for unequal variances; Sokal and Rohlf 1981).

8.4 DISCUSSION

Despite the considerable overlap of lengths of wing chord, outer rectrix length, and primary 8 between sexes it was possible to correctly identify the sex of 82 percent or more of ptarmigan in the same population as the reference collection using a discriminant analysis which incorporated any two of the above three measurements. However, when the analyses were used to determine sex of birds from samples other than the reference collection, the percentage of birds identified correctly changed. As primary 8 was longer in hunted birds than in the reference collection, more females were assigned the incorrect sex. In contrast, in depredated birds males were more often assigned to the wrong sex, as rectrix length in depredated birds was shorter than in the reference collection. The variation in the lengths of measurements are probably due to feather wear. The unpigmented portion of rectrices wears completely between the time they molt in autumn and the following autumn (pers. obs.), reducing rectrix length by several millimetres. Primaries also wear considerably over the year. Moreover, the primaries of males may wear more in spring than those of females, because of wing dragging during courtship. Measurements for the reference collection were all taken in April and May, whereas many of the known-sex depredated birds were found between May and July, and all hunting occurred during the autumn and winter (Chapter 4). In future studies, measurement error in rectrices could be reduced by only measuring the black portion of the rectrix, because it is more resistant to wear than the outer, unpigmented portion (Voitkevich 1966). To reduce variation in length of primaries, measurements for a reference collection should be taken during the same season as birds of unknown sex. When sex ratios are interpreted, differences in timing of collection should be taken into account.

Previously, Bergerud et al. (1963) correctly identified 96 percent of Newfoundland ptarmigan to sex for both age groups, whereas Myrberget et al. (1969) correctly identified 93 percent in Norwegian ptarmigan. West et al. (1968) determined sex of ptarmigan from the Brooks Range, Alaska with an accuracy of 87 percent for yearlings, and 94 percent for adults. All three studies used only wing length and rectrix length. A discriminant analysis was used by Mussehl and Leik (1963) to identify adult blue grouse (Dendrapagus obscurus) to sex. They correctly identified 89.7 percent to sex using primaries 1, 3, and 5. Apparently it was not possible to determine the sex of yearling blue grouse using of this method. None of these studies took feather wear into account.

Wing lengths from Chilkat Pass willow ptarmigan were previously reported by West et al. (1970), who combined them with birds from the southwestern Yukon (Table 8-5). They also recorded tail length, but these measurements could not be compared to data from my study, as they measured tail feathers to their insertion point, whereas I only measured the vane. I found no significant difference in wing chord between birds measured for this study and those measured by West et al. (1970) (t-Test, female juv. $t=0.16$, $P>0.5$; female ad. $t=1.17$, $P>0.10$; male juv. $t=0.12$, $P>0.9$; male ad. $t=1.44$, $P>0.1$), even though they measured wing length, whereas I measured wing chord. The same authors reported that birds from the southwestern Yukon were always smaller than those from the Tanana Valley in eastern Mainland Alaska, but they could not find a significant difference in wing length between birds from the two regions. However, the difference in wing lengths between birds from Chilkat Pass and Tanana was highly significant (t-Test, female juv. $t=4.09$, $P<0.001$; female ad. $t=5.24$, $P<0.001$; male juv. $t=3.26$, $P<0.001$; male ad. $t=5.60$, $P<0.001$). This confirms Aldrich's (1963) classification, which includes willow ptarmigan from Chilkat Pass with L. l. alexandrae

Table 8-5 **Comparison between wing lengths of willow ptarmigan from Chilkat Pass, B.C. and central Alaska**

	Wing length in mm (n)			
Area	Female juv.	Female ad.	Male juv.	Male ad.
Chilkat Pass	179.0 (49)	179.2 (48)	189.3 (50)	189.8 (49)
SW Yukon[1,2]	178.7 (5)	180.8 (3)	188.7 (5)	192.4 (14)
Tanana[2]	184.3 (14)	184.6 (60)	193.6 (27)	195.3 (76)

[1] Data from Chilkat Pass combined with data from SW Yukon.
[2] Data from West et al. (1970).

rather than with *L. l. albus*, as suggested in Fig. 3 of West *et al*. (1970).

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9 APPENDIX 4 ESTIMATION OF SNOWSHOE HARE DENSITIES AT CHILKAT PASS, B.C.

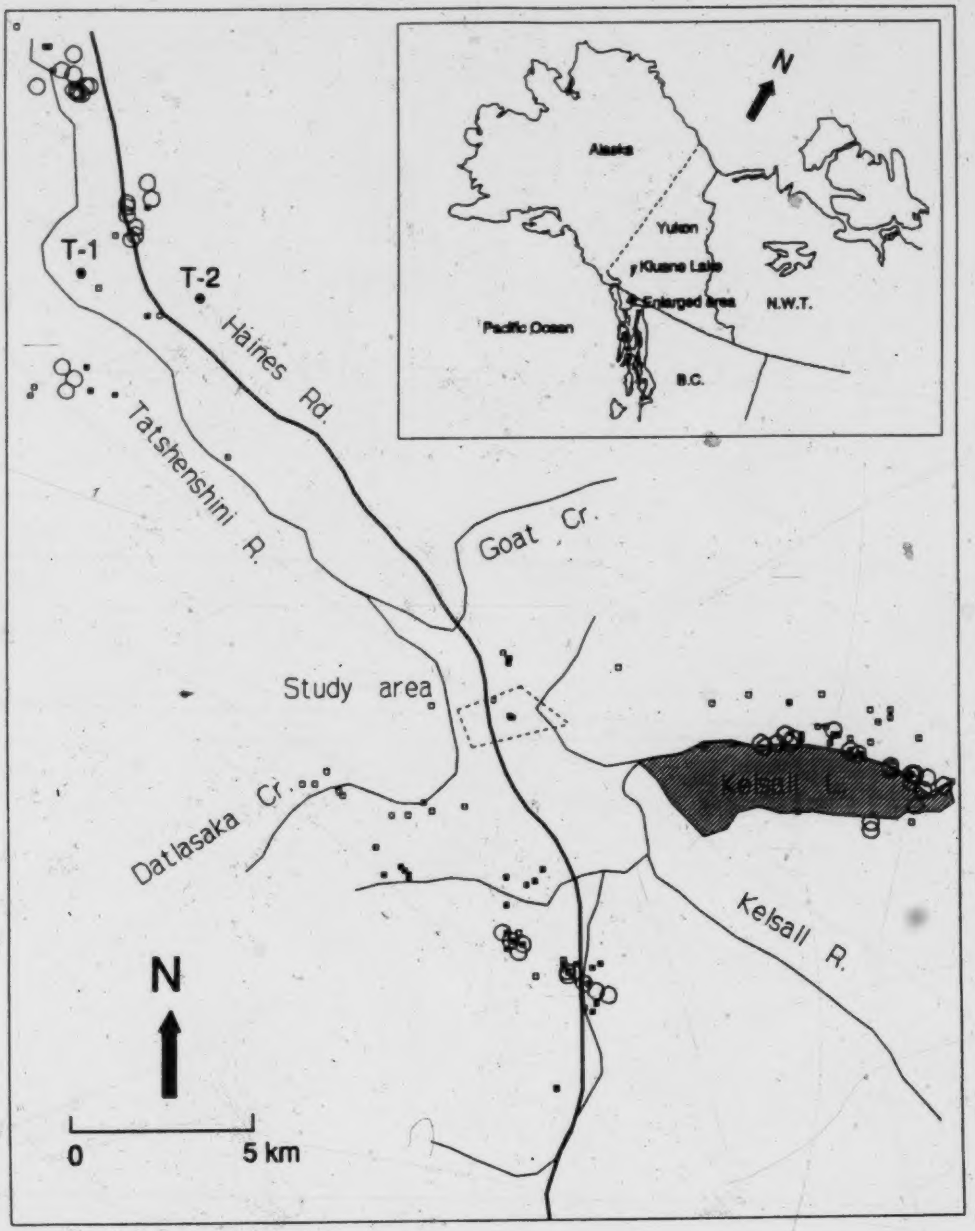
9.1 INTRODUCTION

Numbers of willow ptarmigan (Lagopus lagopus) (Bergerud 1970; Hannon and Barry 1986; Mossop 1987) and snowshoe hares (Lepus americanus) (Keith et al. 1984; Krebs et al. 1986) in North America cycle with a periodicity of 8-11 years. During the winter male ptarmigan remain in alpine areas close to the breeding grounds, whereas most females move to the boreal forest (Chapter 2; Weeden 1964; Höhn 1984; Mossop 1987). It has been suggested that predators in the boreal forest switch to grouse species when populations of hares or voles decline (Hörnfeldt 1978; Angelstam et al. 1984; Keith and Rusch 1986). Hence, females wintering in the boreal forest may suffer higher mortality than males. Moreover, ptarmigan may compete with hares for limited food resources. Consequently, it is important to determine if hares are present on ptarmigan wintering grounds, and if so, what their numbers are.

9.2 METHODS

I estimated the density of snowshoe hares from faecal pellet transects (Krebs et al. 1987) in July of 1987, 1988, and 1990 at two locations at the edge of the boreal forest (Forest Edge; T-1, Figure 9-1; and East Stanley Flats; T-2, Figure 9-1) at Chilkat Pass in northwestern British Columbia (59°50'N, 136°35'W). The topography, vegetation, and climate of the area are described in Appendix 1. At each location I permanently marked 10 transect lines of 10 quadrates of 5.08 x 305cm (Krebs et al. 1987). Quadrates were spaced 15.25m apart, and transect lines 30.48m apart (C.J. Krebs, pers. comm.). The number of faecal pellets in each quadrat was counted in

Figure 9-1 Locations of ptarmigan, Jan.-Feb. 1988 (□), Jan.-Feb. 1989 (■; observations and tracks) and snowshoe hares (O; tracks), Jan.-Feb. 1988. Breeding area of marked ptarmigan is indicated with a square; faecal pellet transects with a T.


Alaska
Yukon
Kluane Lake
Enlarged area
N.W.T.
Pacific Ocean
B.C.
N
T-1
T-2
Haines Rd.
Tatshenshini R.
Goat Cr.
Study area
Datlasaka Cr.
Kelsall L.
Kelsall R.
N
0
5 km

June of 1987, 1988, and 1990. Average hare density (expressed as number of hares/ha) was calculated as follows:

log(hare dens.) = 0.813log($\bar{x}$ faecal pellets/quadr.)-0.236 (C.J. Krebs, pers. comm.).

I determined if snowshoe hares occurred in willow ptarmigan wintering areas by recording hare tracks during field work for a study on winter movements of willow ptarmigan (Chapter 2). Hare tracks were plotted together with observations (sightings and tracks) of willow ptarmigan (Chapter 2).

9.3 RESULTS AND DISCUSSION

The densities of hares at the edge of the boreal forest were similar in 1987 and 1988, but they increased in 1990 (Table 9-1). Densities of hares at both sites on the edge of the boreal forest were lower than at Kluane Lake 100km to the northwest (C.J. Krebs, pers. comm.). Differences in hare densities between the two pellet transects at the forest edge, and between Chilkat Pass and Kluane Lake probably reflected differences in habitat quality.

In both winters I found snowshoe hares in areas where both sexes of willow ptarmigan wintered (Figure 9-1). However, hare densities in subalpine habitats, where most males winter, may be lower than in the boreal forest, as subalpine habitat was similar to that at the forest edge. Gelting (1937) and Bossert (1980) reported that the winter ranges of rock ptarmigan and snowshoe and mountain hares (L. timidus), respectively, overlapped. However, Bossert (1980) observed no food competition between the two species. Although densities of hares at both sites on the edge of the boreal forest were lower than at Kluane Lake, in 1988-89 radio-tagged ptarmigan moved as far as 60km past the edge of the boreal forest (Chapter 2), where hare densities may be similar to those at Kluane Lake. In years with heavy snowfall

Table 9-1 **Hare densities on faecal pellet transects (Krebs et al. 1987) at Chilkat Pass, B.C. 1986-87, 1987-88, and 1989-90**

	Forest Edge		East Stanley Flats	
Year	Hares/ha	95% CI	Hares/ha	95% CI
1986-87	0.48	0.37-0.61	0.12	0.09-0.18
1987-88	0.22	0.16-0.30	0.08	0.05-0.12
1989-90	0.92	0.72-1.16	0.44	0.34-0.56

ptarmigan from Chilkat Pass probably move farther. Willow and rock ptarmigan have been recorded throughout the northern prairie provinces and northern Ontario, as far as 500km from their breeding ranges (Lumsden 1964; Höhn 1977; Pulliainen 1980; Höhn 1984). If a snow rich year coincides with high hare density in the Yukon, the two species may well compete for limited food resources.

During the two years of the study I observed no difference in mortality between ptarmigan that moved to the boreal forest and those that remained in alpine habitat (Chapter 3). However, during the study the numbers of snowshoe hares in the boreal forest were increasing, and thus predators may have preyed on the more numerous hares. Once the hare population declines, predators may switch to ptarmigan wintering in the boreal forest (Keith and Rusch 1986; see Hörnfeldt 1978 and Angelstam et al. 1984). Therefore, changes in hare numbers may contribute to changes in predation of ptarmigan.

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10 APPENDIX 5 INFORMATION SHEETS GIVEN TO HUNTERS

ATTENTION HUNTERS

I am back again this winter to study willow ptarmigan at 80 mile (north of Mule Creek Highway camp). I really appreciate all the help I got from you last winter! The wings have helped me find out where ptarmigan spend the winter and what happens to them. Again this winter I would like you to leave the entire right wing of any ptarmigan you shoot at Canada Customs. There are plastic bags with tags at Customs.
Although I am most interested in willow ptarmigan, I want to keep track of all three species of ptarmigan. However, sometimes it is difficult to tell from the wings what the species is. Therefore, could you please indicate the species (when possible) on the tag, along with when and where (approximately) you shot the birds?
To tell the species apart:

White-tailed ptarmigan: - white tail.
Rock ptarmigan: - black tail.
- fall: difficult to tell apart from willow ptarmigan. (smaller, and smaller bill)
- winter: males have black stripe from bill to eye. Females don't have the black stripe, and are difficult to tell apart from willow ptarmigan.

Willow ptarmigan: - black tail
- winter: no black stripe through eye.

If you shot any willow ptarmigan with numbered legbands or radio transmitters, could you please leave those with the wing of the bird at customs as well? The transmitters are a package of 1/2" x 1/2" x 1" that hangs around the neck of the bird.

If you have any further questions, or if you would like more information, please leave your name and address at Customs, so I can contact you. (If you filled out a form last year, but did not hear from me yet, please fill out this form, and I will be in touch with you shortly.)

Thank you for your cooperation,

Rogier Gruys
Dept of Zoology
Univ. of Alberta

Local address:
Box 5310
Haines Junction, Yukon Y0B 1L0

* * *

I would like more information on the willow ptarmigan research project.

NAME: ______________________ PHONE # ______________

MAILING ADDRESS: ______________________

* * *